PATTERNS OF AND CONTROLS OVER NITROGEN INPUTS BY GREEN ALDER (*ALNUS VIRIDIS* SPP. *FRUTICOSA*) TO A SECONDARY SUCCESSIONAL CHRONOSEQUENCE IN INTERIOR ALASKA

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A

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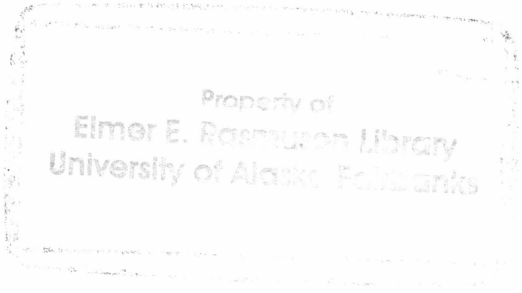

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ABSTRACT

Patterns of and controls over N_2 fixation by green alder (*A. viridis*) were studied in post-fire, mid-succession, and white spruce upland forests in interior Alaska during 1997-2000, focusing on the hypothesis that ecosystem-level nitrogen (N) inputs decrease with successional development. Across all stands, alder created islands of elevated soil N and carbon, depleted soil phosphorus (P), and more acidic soils, effects which translated to the stand-level in response to greater alder stem density. Rates of N_2 fixation (measured by acetylene reduction = ARA) closely tracked plant phenology during the 1997 (a drought year) and 1998 (a year of normal precipitation) growing seasons. During 1998, stands with higher maximum ARA had higher %N in the O, A, and C soil horizons. N_2-fixation rates were influenced by soil P, as evidenced by the findings that maximum ARA was positively correlated with foliar N:P ratios, and with subcanopy %P in the O and A soil horizons. During the drought year, alder leaf %P and leaf N resorption were lower and leaves were thinner when compared to 1998. Drought effects were most pronounced in mid-succession where alder exhibited reduced ARA (-76%), leaf %P (-14%), leaf thickness (-40%), and lower leaf resorption of P (-66%) and N (-78%). Although ARA and nodule biomass did not differ among stand types, increases in alder densities with successional time translated to increasing ecosystem-level N inputs across the chronosequence. These results contradict established theory predicting a decline in N_2-fixation rates and N_2-fixer abundance during successional stand development.

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INTRODUCTION

Supply of fixed nitrogen (N) to forest ecosystems regulates species composition (Post and Pastor 1996), net primary production (Vitousek and Howarth 1991), rates of succession (Chapin et al. 1994), and landscape evolution (Hu et al. 2001). In addition to direct effects on ecosystem N budgets (Binkley et al. 1992, Helfield and Naiman 2002, Uliassi and Ruess 2002) and productivity (Bormann et al. 1994, Binkley 2003), N_2-fixing plants also have strong indirect effects on soil physiochemical characteristics (Rhoades et al. 2001), including soil carbon (C) stocks (Rhoades et al. 1998, Resh et al. 2002) and pathways of N fluxes within ecosystems (Hart et al. 1997, Rhoades et al. 2001). For example, high rates of N_2 fixation are often associated with increased rates of nitrification, denitrification (Pastor and Binkley 1998, Kielland et al. 2006), and soil acidification (Van Migroet and Cole 1984, Binkley and Sollins 1990, Rhoades et al. 2001). N_2-fixing species are also responsible for strong interactions between N and phosphorus (P) cycling, because of the high P requirements of nodule development and growth as well as nitrogenase activity (Wall et al. 2000, Huss-Danell et al. 2002, Vitousek et al. 2002), and the capacity of these species to increase P cycling through elevated soil phosphatase activity (Zou et al. 1995, Giardina et al. 1995). Moreover, rates of N_2 fixation in tropical (Crews et al. 1995, Vitousek and Hobbie 2000, Binkley et al. 2003), temperate (Binkley et al. 1994), and boreal (Uliassi and Ruess 2002) forests are often limited by plant-available soil P.

Although the significance of N_2-fixing plants to the N economy of terrestrial ecosystems is broadly recognized, the ecological factors regulating inputs via N_2 fixation have never been fully characterized for any ecosystem (Vitousek and Field 1999, Vitousek et al. 2002). There are several reasons for this. First, many N_2-fixing plants form additional symbioses with arbuscular (Shirihari et al. 2000) or ectomycorrhizal (Yamanaka et al. 2003) fungi, making the molecular, biochemical, and ecophysiological mechanisms affecting these tripartite relationships extremely complex. This complicates predictions of the role of ecological factors such as light availability, climate regime, herbivory, and soil nutrient status, all of which affect plant growth, demand for N, nitrogenase activity and thus associated ecosystem N inputs (Vitousek et al. 2002, Vitousek and Field 1999, Ruess et al. 2006). Secondly, several key parameters necessary for scaling physiological measures to stand-level N inputs, particularly nodule biomass, are logistically challenging to sample. Finally, interactions among regulating factors are often ecosystem specific (Vitousek et al. 2002) and can change substantially over short periods of successional time (Uliassi and Ruess 2002). These reasons explain why temporal and spatial patterns of potentially limiting environmental factors typically account for less than half the variation in N_2 fixation rates at the nodule or stand scales.

Throughout interior Alaska, N_2 fixation by *Alnus* spp. is the primary pathway for ecosystem N accumulation during primary succession in floodplain environments and during secondary succession following fire in upland landscapes (Van Cleve et al. 1983, Uliassi and Ruess 2002). On river floodplains, N_2 fixation by thin-leaf alder (*Alnus incana ssp. tenuifolia*, hereafter, *A. tenuifolia*) declines from early to mid succession, due

to reductions in both nitrogenase activity and alder stem density (Uliassi and Ruess 2002, Anderson et al. 2004). Uliassi and Ruess (2002) reported 30% reductions in acetylene reductase activities and 36% reductions in area-based N inputs in mid-succession stands, where *A. tenuifolia* occupies the sub-canopy of balsam poplar (*Populus balsamifera*), relative to early succession stands, where *A. tenuifolia* can form a near-continuous canopy. Reasons for this down-regulation of nitrogenase in mid-succession balsam poplar stands likely include reduced alder growth and alder plant N demand, driven by lower light availability and perhaps colder soils. As with many other N_2-fixing species, N_2 fixation rates in *A. tenuifolia* are governed by plant N to P stoichiometry (Huss-Danell 1997, Uliassi and Ruess 2002, Valverde and Wall 2003), and are thus influenced strongly by soil P availability (Huss-Danell et al. 2002, Valverde et al. 2002, Vitousek et al. 2002, Gentili and Huss-Danell 2003). Uliassi and Ruess (2002) reported that stimulation of N_2 fixation by P fertilization was less during mid-succession, also pointing to growth limitation due to other factors. This pattern of reduced N_2-fixation input over successional time has been noted for a number of temperate ecosystems (Vitousek and Howarth 1991, Chapin et al. 1994, Vitousek and Field 1999, Vitousek et al. 2002).

Green alder (*A. viridis spp. fruticosa,* formerly *A. crispa*, hereafter *A. viridis*) is the most widely distributed alder species within interior, western, and northern Alaska. This species is a sub-canopy dominant shrub in both white spruce (*Picea glauca*) and black spruce (*Picea mariana*) forests, and resprouts vigorously following fire, serving as a keystone species in early successional dynamics (Walker 2006). *A. viridis* also dominates the shrub canopy at both latitudinal and elevational treelines, and occupies

broad expanses of arctic shrublands where its range has expanded significantly over the past century (Sturm et al. 2001, Tape et al. 2006). The likelihood that this range expansion is a consequence of recent high latitude warming (Sturm et al. 2005) is supported by correlations between regional climate gradients and modern pollen assemblages of *Alnus* throughout northern Alaska (Oswald et al. 2003) and the expansion of *Alnus* concurrent with warmer and wetter conditions during the Holocene (Edwards et al. 2001, Oswald et al. 2003). Lloyd et al. (2005) reported both positive and negative growth responses of individual white spruce treeline stands against a backdrop of regional warming and treeline advance. Whether there are similar thresholds of warming beyond which *Alnus* response to climate is no longer positive remains unknown.

Although *A. viridis* is known to influence the N economy of Alaskan boreal forests (Van Cleve et al. 1986, Wurtz 1995, Rhoades et al. 2001, Anderson et al. 2004), no study has quantified N_2-fixation inputs by the species across a complete secondary successional sequence or assessed the magnitude of inputs in upland white spruce forests where the species is so abundant. My foremost goal was to describe patterns of N_2 fixation across an upland successional sequence in interior Alaska. I used acetylene reduction to estimate ecosystem-level N inputs and assess controls over N_2 fixation by *A. viridis* along a gradient of stands representing three successional stages of post-fire forest development. The specific objectives were to (1) characterize seasonal patterns of N_2 fixation rates across a 200-year old upland forest successional sequence, (2) evaluate climatic and stand-character controls over N_2 fixation rates and selected plant ecophysiological traits important to alder growth, and (3) assess the effects of *A. viridis*

on canopy-level and stand-level N, P and C soil parameters across the successional sequence. I sought to test the following hypotheses; H1: Soil nutrient availability (mainly N and P), in conjunction with micro-climate (mainly soil temperature and moisture), regulates alder ecophysiology and associated N_2 fixation rates, H2: Alder has strong direct and indirect effects on soil chemical properties, and H3: Ecosystem-level N inputs decrease with secondary successional stand development of upland forests within interior Alaska.

STUDY AREA

Study stands representing seral stages of upland secondary successional forests were selected within the Bonanza Creek Experimental Forest (BCEF) located approximately 35 km southwest of Fairbanks, Alaska (64.8 ° N, 148.0 ° W). Replicate (n=3/stage) stands of a seral sequence of successional stages are maintained within the BCEF by the Bonanza Creek Long-Term Ecological Research program (BNZ LTER); more detailed information regarding the stages described below can be found on the BNZ LTER webpage (http://www.lter.uaf.edu). I began my investigation in 1997, 14 years after the 1983 Rosie Creek fire burned extensive portions of the BCEF. I believe that alder individuals in this study are the current aboveground production of alder rootstocks (individuals) which inhabited the same area prior to fire disturbance (Wurtz 2000). Early succession (post-fire) stands were open, rapidly developing deciduous canopies with a dense herbaceous (*Epilobium angustifolium*) and graminoid (*Calamagrostis canadensis*) ground cover surrounding numerous but scattered *A. viridis* and willow (*Salix* spp.) shrubs, with isolated recruitment pockets of white spruce, paper birch (*Betula papyrifera*)

and trembling aspen (*Populus tremuloides*) saplings. Prior to the 1983 fire these stands were dominated by mature white spruce (basal area ~ 35 m^2 ha^{-1}) with some paper birch (http://www.lter.uaf.edu). In open-canopy post-fire environments, *A. viridis* grows as isolated shrubs with upright densely-clustered stems up to 5 m in height. Mid-succession stands (~ 60 years old) were dominated by paper birch, white spruce, and trembling aspen with basal areas of 18.5, 7.1, and 0.6 m^2 ha^{-1}, respectively (http://www.lter.uaf.edu). The understory tall shrub community consists of *A. viridis* and willow. On drier, south-facing slopes in early- and mid-succession communities, aspen dominates the overstory, and *A. viridis* is restricted to mesic drainages at the base of hillslopes. I avoided these stands, and selected more mesic stands, where alder was more abundant. Late succession conifer stands (~220 years old) were dominated by white spruce (basal area ~ 30 m^2 ha^{-1}) (http://www.lter.uaf.edu), with a discontinuous understory of *A. viridis*, and a near-continuous ground cover of feathermoss (*Hylocomium splendens* and *Pleurozium schreberi*). In mid-and late-succession stands, *A. viridis* is a prominent understory shrub (up to 5 m in height) with a somewhat disorderly arrangement of fewer thicker stems. This growth morphology appears to be a function of the species' ability to both exploit overstory gaps and propagate vegetatively from prostrate stems. Across the successional sequence, soil parent material is glacially-formed loess, and soils are referred to as Fairbanks silt loam and classified as Alfic cryochrept (Viereck et al. 1983). My replicate stands within each of these seral successional stages correspond to BNZ LTER designated successional stages UP1, UP2 and UP3 which I will henceforth refer as *post-fire*, *mid-succession*, and *white spruce* stages, respectively.

Climate in interior Alaska is strongly continental with extremely cold winters and dry warm summers. Air temperature ranges from -50°C to +33°C with an annual average of -2.9°C and the frost free growing season averaging approximately 100 days. Summer daylight hours are long (up to 21 hours per day), and the region receives an average of 289 mm of precipitation annually, 60% of which falls as rain (Viereck et al. 1993). Well-drained soils are associated with the topographically variable upland stands within the BCEF, where vegetation on south-facing slopes is particularly subject to drought stress during low precipitation years. In response to the regional warming and drying of recent decades, periodic drought stress has reduced aboveground growth of white spruce across interior Alaska (Barber et al. 2000).

I measured a number of climatically-sensitive and seasonally-variable ecophysiological traits of *A. viridis* over the 1997 and 1998 growing seasons. It is noteworthy that interior Alaska received an unusually low amount of both annual and summer precipitation during my first study year compared with the second year of study when rainfall was close to the decadal average (Figure 1) (http://climate.gi.alaska.edu). My study area received approximately three times more summer precipitation in 1998 than in 1997 (http://www.lter.uaf.edu) (Figure 2). Moreover, seasonal maximum soil temperatures at 10 cm soil depth were higher in the wetter year of 1998 (11.5 ± 0.3 °C) than in dry 1997 (9.9 ± 0.5 °C). Across both years, soil temperatures during the growing season were higher in mid-succession stands (12.1 ± 0.4 °C) compared to white spruce (10.3 ± 0.5 °C) and post-fire (9.7 ± 0.6 °C) stands (http://www.lter.uaf.edu).

METHODS

Experimental design

In May of 1997 I selected three replicate stands within each of the three successional stages described above. All stands were located within 10 km of one another and had slopes ranging from 10° to 30° with a predominantly southerly aspect. Where possible I utilized previously established and monitored BNZ LTER stands. *A. viridis* was absent in one replicate from the post-fire (UP1C) and mid-succession (UP2C) replicate stands, likely due to competition for water with a dense aspen overstory. Therefore, I substituted these stands with two additional stands where *A. viridis* was present and which closely resembled and were near to the established BNZ LTER stands.

At each of the nine stands I selected a total of 70 *A. viridis* shrubs over an area of approximately 2.5 ha. During each of seven sampling periods over two growing seasons (Table 1), I randomly selected 10 of the 70 *A. viridis* shrubs from each replicate stand for measurement of N_2 fixation, foliar morphology and chemistry, as well as concurrent soil temperature. An average of 1.5 days was required to complete the sampling of 10 shrubs for each replicate. To ensure sufficient resolution of seasonal trends for each stage, I staggered sampling of replicate stands within each stage; that is, I visited one post-fire replicate, then one mid-succession replicate, then one white spruce replicate stand, repeating this pattern until all nine stands had been visited once within a sampling period. All sampling took place between 10:00 and 19:00 (Alaska Standard Time).

I also established three parallel 10 m X 100 m plots with a north-south orientation at each replicate stand (n = 27). These plots were located close to but not overlapping the areas used for nodule collection (described below). These plots were visited in September 1999 to collect soil cores for determination of nodule biomass and soil chemical characteristics, and again in autumn of 2000 to record alder density and canopy cover.

Nitrogenase activity

Nitrogen fixation rate per unit nodule biomass was assessed using a modified short-term acetylene reduction assay (ARA) following the protocol of Uliassi and Ruess (2002). Nodule samples of 1-2 g dry weight were collected from the top 15 cm of soil within 2 m of the shrub base, dusted free of soil and placed in a 60 mL incubation syringe and temporarily stored below the soil surface to maintain subsurface nodule temperatures. Nodule collection required up to 25 minutes per shrub. Assays were initiated by injecting acetylene (C_2H_2) (generated from CaC_2 in a Bliss generator) to create a 10% acetylene to air (v/v) gas mixture within the syringe. Gas samples (6 ml) were withdrawn at 30 and 90 seconds and stored in clean 10 mL syringes fitted with stopcocks. Gas samples were transported to the laboratory, stored at 4 °C for a maximum of 3 days, and then analyzed for ethylene (C_2H_4) concentration. Nodule samples utilized in the assay were transported to the laboratory, thoroughly washed of soil, dried at 60 °C, and weighed to the nearest 0.1 mg.

Gas analyses were conducted using a Shimadzu 14A gas chromatograph (Shimadzu Scientific, Houston, Texas, USA) fitted with a 2-m Poropak N column and a back-flush valve to vent excess C_2H_2. To calculate nitrogenase activity, I regressed the molar concentration of C_2H_4 in each 6 mL syringe against sampling time, forcing the regression through the origin. The slope of this relationship for each plant was then divided by the associated nodule dry weight and reported as acetylene reductase activity (ARA = μmol C_2H_4 g nodule^{-1} hr^{-1}). I initially followed the protocol outlined by Uliassi and Ruess (2002), who sampled incubations after 30, 90, and 150 seconds following C_2H_2 injection. However, because omission of the 150 s gas sample did not significantly change the slope of the incubation relationship, I elected to collect and analyze only 30 and 90 second samples. Concurrent to each field ARA measurement I recorded soil temperature at a depth of 10 cm at two undisturbed locations beneath the alder canopy using an analog soil thermometer.

Foliar chemistry and morphology

Immediately following each field sampling of ARA, and thus throughout the growing season, I collected leaf samples from associated alder individuals. All leaf samples were from the third fully-expanded leaves on branches of haphazardly chosen alder stems. One 2 cm diameter punch was removed from the center of each of five leaves for a pooled calculation of leaf specific weight (SLW = g m^{-2}), and an additional five intact leaves were collected and pooled from each plant for chemical analyses.

Pooled leaf samples were oven-dried for 48 hours at 60 °C, and ground using a Wiley mill (850 μm mesh). Leaf N content (%N) was determined using a LECO CNS 2000 autoanalyzer (LECO, St Joseph, Michigan, USA), and leaf P content (%P) was determined colorometrically following perchloric acid digests using a modified Technicon autoanalyzer (Whitledge et al. 1981). Leaf nutrient content (g m^{-2}) was calculated by multiplying foliar nutrient concentrations by SLW.

I report foliar N and P resorption as resorptive pool size (mass of nutrient resorbed per unit leaf area) and resorption efficiency (percentage of pool size resorbed). Resorptive pool sizes were calculated by subtracting senescent foliar nutrient content from seasonal maximum foliar nutrient content. In the rare case where senescent leaf nutrient content was higher than seasonal maximum leaf nutrient content, I defined resorption as zero.

Soil physical and chemical parameters

In September of 1999 I collected soil cores to identify stage, replicate stand, canopy, and soil horizon patterns of soil physical and chemical parameters. A pair of cores (5 cm in diameter by 20 cm in length) was collected for each of five haphazardly selected *A. viridis* individuals within each study plot. Soil core pairs included one core taken beneath the alder canopy within 2 m of the alder base, and a second core taken from interspace soils approximately 2 m beyond the alder canopy perimeter. Soil cores were transported to the laboratory and frozen intact. Once thawed, the vertical thickness

of each horizon was measured, and the core was separated by horizon. The forest floor organic (O) horizon was comprised of Oi, Oe, and Oa horizons. Mineral A and C horizons were defined by the color of field moist soils (Munsell Color Company 1992). Where a distinct C horizon was absent the entire mineral soil was referred to as the A horizon. Mineral soil samples were sieved through a 2 mm mesh to remove coarse fragments. Each soil sample (soil core horizon) was oven-dried separately at 60° C for 96 hours, weighed for calculation of bulk density and analyzed for chemical characterization. Each sample was analyzed for total N and C concentrations using a LECO CNS 2000 autoanalyzer. Total soil phosphorus was determined colorometrically following perchloric acid digests as outlined above for leaf tissue. Soil pH was determined on a 1:2 (v/v) soil:water suspension.

Nodule biomass and N inputs

Nodule biomass was sampled in September 1999. At each replicate, one soil core (15 cm diameter x 20 cm deep) was removed from beneath the canopy (within 1.5 m of the central bole) of two of the five alders selected for the above-described nutrient analyses. Nodule biomass cores were transported to the laboratory and frozen. Thawed cores were washed clean of soil to isolate roots and nodules, and then sorted to separate nodules from roots. Nodule samples were oven-dried at 60 °C for 48 hours and then weighed to the nearest 0.1 mg. In the autumn of 2000 I revisited the study plots to record

alder plant density, the number of stems per plant, and the diameter of each alder stem ≥ 1 cm diameter at a height 1 m above the stem-soil interface.

To estimate annual N inputs from N_2 fixation, I first fit a spline interpolation function to seasonal patterns of ARA for each stand in order to estimate daily input values, setting ARA values at zero for 21 May and 1 October. I then used the C_2H_2 to N_2 reduction ratio of 2:1 determined by Anderson et al. (2004) for *A. viridis*, and assumed that my measurements of ARA were representative of rates throughout each 24-hour period. Total annual N inputs for each replicate stand (kg N m^{-2} yr^{-1}) were then obtained by multiplying N inputs per unit nodule biomass times nodule biomass per unit area (described below).

Statistical analyses

SAS 9.1 (SAS Institute 2001) was used for all statistical analyses. Main treatment effects on plant parameters (successional stage, sampling period, and year) were tested using ANOVA (PROC GLM), with individual alder shrubs nested within stands, with stands being the level of replication. Treatment effects (successional stage and canopy location) on soil parameters were also analyzed using ANOVA (PROC GLM) with soil cores nested within stands and stands as the level of replication. Any significant effects from general linear models were subsequently examined with a Tukey's HSD test.

I used Spearman's correlation (PROC CORR) to examine possible relationships between soil and plant parameters (i.e., seasonal maximum values of plant parameters

and alder stem density). To explore relationships between plant parameters and stand-level soil properties I pooled data for canopy and interspace soils. Annual seasonal maximum values of plant parameters (i.e., ARA, leaf % N, leaf % P, SLW and soil temperature) were isolated as the highest average value for a single sampling period at a given replicate (n = 10 alders).

To define primary controls over N_2 fixation, stepwise regression was used to evaluate the combined effects of linear and quadratic terms for soil temperature and Julian day across all plants. Data were tested for normality using PROC UNIVARIATE, and transformed where necessary to meet statistical assumptions (Zar 1984). Significance for all tests was set at $P < 0.05$; however, I included "marginally significant" values ($P < 0.10$). Unless otherwise stated, values throughout the text are untransformed and represent means ± 1 standard error.

RESULTS

Soil properties

Data for soil bulk density and soil mass to a depth of 20 cm for each successional stage are reported in Table 2. Variations in soil chemical properties across successional stages are presented in Table 3. Soil N of the top 20 cm was lowest in the mid-succession (209 ± 12 g m^{-2}), and did not differ significantly between post-fire (242 ± 12 g m^{-2}) and late-succession white spruce (274 ± 14 g m^{-2}) stages ($F_{2,25} = 5.84$, $P < 0.05$) (Figure 3, Table 3). Soil C content did not differ between post-fire (3674 ± 246 g m^{-2}) and mid-succession stands (3902 ± 217 g m^{-2}) but was higher in white spruce stands

(4821 ± 203 g m^{-2}) ($F_{2,25}$ = 14.30, P < 0.0005) (Figure 3). Soil C:N ratio was lowest in the post-fire stage (15.2 ± 0.6) compared to mid-succession (19.1 ± 0.8) and white spruce (18.3 ± 0.7) stages which did not differ. Total soil P content of the top 20 cm declined significantly with transition from post-fire (79.1 ± 3.0 g m^{-2}) to mid-succession (54.6 ± 3.2 g m^{-2}) and white spruce (44.4 ± 3.1 g m^{-2}) stages ($F_{2,25}$ = 34.55, P < 0.0001) (Figure 4). Soil pH ranged from 4.9 to 6.8 across successional stages and soil horizons (Table 5).

Alder stem density and canopy effects on soil properties

A. viridis shrub density increased over successional time, averaging 90.0 ± 9.9, 178.9 ± 30.1 and 290.0 ± 62.3 shrubs ha^{-1} for post-fire, mid-succession and white spruce stages, respectively ($F_{2,26}$ = 20.08, P < 0.0001) (Table 4). However, due to variation in alder stem numbers per plant among stages (21.1 ± 2.2, 5.1 ± 0.3 and 13.1 ± 1.3 stems $plant^{-1}$ in post-fire, mid-succession and white spruce stages, respectively) stem density was highest in white spruce stands (3630.0 ± 720.4 stems ha^{-1}), intermediate in post-fire (1805.6 ± 175.5 units) and least in mid-succession stands (897.8 ± 162.5 units) ($F_{2,26}$ = 31.34, P < 0.0001).

O horizon mass under alder canopies did not differ from non-canopy soils (Table 5). Only in white spruce stands with a near-continuous moss layer over interspace soils did subcanopy soils have lower O horizon mass ($F_{1,28}$ = 4.75, P < 0.05) (Table 6C) with lower bulk density ($F_{1,28}$ = 6.98, P < 0.05). Alder stem density was positively correlated

with O horizon mass (g m^{-2}) across stages ($r^2 = 0.49$, $P < 0.0001$), in white spruce stands ($r^2 = 0.77$, $P < 0.05$) and marginally in post-fire stands ($r^2 = 0.35$, $P < 0.10$).

Carbon concentration of subcanopy O horizon soils was elevated relative to non-canopy soils when averaged across all stages, ($F_{1,90} = 5.04$, $P < 0.05$) (Table 5) and marginally in post-fire stands ($F_{1,33} = 3.31$, $P < 0.10$) (Table 6A). However, these values did not necessarily translate to higher subcanopy O horizon C content. Alder stem density related positively to O horizon ($r^2 = 0.37$, $P < 0.005$) (Figure 5A) and total ($r^2 = 0.22$, $P < 0.05$) soil C content (g m^{-2}) (Figure 5B) across all stages. These relationships between stem density and organic and total soil C content were also evident among post-fire stands ($r^2 = 0.69$, $P < 0.05$, and $r^2 = 0.39$, $P < 0.10$, respectively). Alder stem density in mid-succession stands was positively correlated only with mineral soil % C ($r^2 = 0.54$, $P < 0.05$). In white spruce stands, alder stem density was inversely correlated with organic soil %C ($r = -0.73$, $P < 0.05$).

When averaged across all stands and successional stages % N of organic soil under alder canopies was significantly greater than in interspace soils ($F_{1,90} = 6.56$, $P = 0.05$) (Table 5), but this difference was driven principally by a strong effect in white spruce stands ($F_{1,26} = 9.80$, $P < 0.005$) (Table 6C). Subcanopy depletion of soil N content was detected only in mid-succession stands, where A horizon N content (g m^{-2}) was 28% lower under alder canopies compared with interspace soils ($F_{1,29} = 3.09$, $P < 0.10$) (Table 6B). Alder canopies did not have an effect on soil C:N ratios across successional stages nor among post-fire and mid-succession stands; only in white spruce

stands was an alder canopy associated with islands of reduced O horizon ($F_{1,26} = 5.04$, $P < 0.05$) and total soil ($F_{1,26} = 4.14$, $P = 0.05$) C:N ratio (Table 6C).

Alder stem density related positively to O horizon ($r^2 = 0.35$, < 0.005) (Figure 5C) and total soil ($r^2 = 0.20$, $P < 0.05$) N content (g m^{-2}) across all replicate stands. Within successional stages, these relationships were most evident in post-fire stands ($r^2 = 0.72$, $P < 0.005$ and $r^2 = 0.35$, $P < 0.10$, respectively). In mid-succession stands, alder stem density correlated positively with stand-level O horizon ($r^2 = 0.37$, $P < 0.10$) and A horizon ($r^2 = 0.45$, $P < 0.05$) % N. In contrast, alder stem density in white spruce stands was inversely correlated with % N of O horizon ($r = -0.89$, $P < 0.005$) and A horizon ($r = -0.86$, $P < 0.05$) soils, as well as with C horizon N content ($r = -0.66$, $P < 0.10$) but related positively to organic soil N content ($r^2 = 0.49$, $P = 0.05$).

Across all successional stages, alder created islands of acidified C horizon soils ($F_{1,79} = 6.72$, $P < 0.05$); the same effect was marginally evident in A horizon soils ($F_{1,90} = 3.38$, $P < 0.10$) (Table 6). Patterns were most apparent in post-fire stands, where alder acidified O ($F_{1,33} = 5.09$, $P < 0.05$), A ($F_{1,33} = 6.98$, $P > 0.05$) and C ($F_{1,24} = 4.82$, $P < 0.05$) horizon sub-canopy soils (Table 6A). Across all stages, greater alder stem density was associated with lower C horizon pH ($r = -0.41$, $P < 0.05$). This relationship was most apparent within the mid-succession stage, where alder stem density was associated with lower soil pH in both the O ($r = -0.67$, $P < 0.05$) and C ($r = -0.60$, $P < 0.10$) horizons, and was also evident in white spruce stands but only for A horizon soils ($r = -0.65$, $P < 0.01$).

Across all stands, the phosphorus content of total ($F_{1,90} = 4.96$, $P < 0.05$) and C horizon ($F_{1,90} = 5.79$, $P < 0.05$) soils was lower under alder canopies than for interspace soils (Table 5). This effect was greatest in mid-succession where alder created islands of depleted total ($F_{1,29} = 5.82$, $P < 0.10$) (Figure 4, Table 6B) and C horizon ($F_{1,29} = 4.93$, $P < 0.05$) soil P content (g m^{-2}) (Table 6B). Alder presence in white spruce stands was also associated with a marginally significant depletion of C horizon P content ($F_{1,24} = 3.21$, $P < 0.10$) (Table 6C).

Patterns and controls over nitrogen fixation

Seasonal patterns of ARA closely tracked plant phenology throughout the growing season. Rates were relatively low early in the growing season, averaging 1.82 ± 0.29 μmol C_2H_4 g $nodule_{DWT}^{-1}$ hr^{-1} on 15 June, approximately 3 weeks following leaf-out. Highest ARA rates were measured during the third week of July (7.93 ± 0.89 μmol C_2H_4 g $nodule_{DWT}^{-1}$ hr^{-1}), and rates declined to 0.76 ± 0.11 μmol C_2H_4 g $nodule_{DWT}^{-1}$ hr^{-1} by September. Across all samples, ARA varied more over the course of growing seasons ($F_{5,540} = 36.65$, $P < 0.0001$) (Figure 6A-C) than between years ($F_{1,540} = 0.01$, $P = 0.92$), stages ($F_{2,540} = 5.74$, $P < 0.005$), or replicates within stages ($F_{6,540} = 3.34$, $P < 0.005$).

Over both growing seasons, variability in soil temperature explained a relatively small proportion of the variation in ARA across all replicate stands and sampling periods (all $r^2 = 0.10$, $P \leq 0.05$). However, the best model for predicting ARA (μmol C_2H_4 g $nodule_{DWT}^{-1}$ hr^{-1}) across all stands and sampling periods included a linear response to soil

temperature (SOILT, °C) and a quadratic response to julian day (DAY) ($r^2 = 0.23$, $P < 0.0001$).

$$ARA = -0.113*SOILT + 0.757*DAY - 0.0018*(DAY)^2 - 71.897$$

Seasonal maximum rates of ARA correlated positively to soil temperature across years and stages ($r^2 = 0.40$, $P < 0.005$) (Figure 7), within 1997 ($r^2 = 0.35$, $P < 0.10$) and 1998 ($r^2 = 0.37$, $P < 0.10$), and across years among mid-succession stands ($r^2 = 0.79$, $P < 0.05$). I believe that these positive correlations were partially the response of alder to water availability since rainfall and soil temperature were both elevated in 1998 compared to 1997.

I detected no successional trend in seasonal maximum values of ARA, which averaged 6.54 ± 0.63, 5.13 ± 0.81, and 6.32 ± 0.59 μmol C_2H_4 g $nodule_{DWT}^{-1}$ hr^{-1} for post-fire, mid-succession and white spruce stages, respectively ($F_{2,17} = 1.51$, $P = 0.28$) (Figure 8). Nor was there a significant overall difference in maximum ARA between study years ($F_{1,17} = 2.99$, $P = 0.12$) or among replicates within stages when all data were combined. Interannual difference in seasonal maximum ARA within a successional stage was only significant in mid-succession where alder exhibited lower ARA during the dry year, 1997 (3.73 ± 0.17 μmol C_2H_4 g $nodule_{DWT}^{-1}$) compared to 1998 (6.53 ± 1.14 μmol C_2H_4 g $nodule_{DWT}^{-1}$) ($F_{1,5} = 5.88$, $P < 0.10$), the year of normal precipitation (Figure 8).

Across years and successional stages there were few significant relationships between seasonal maximum values for ARA and measured plant parameters (i.e., leaf

%N, leaf %P, leaf N and P resorptive pools and efficiencies). However, I did detect an inverse correlation between foliar N:P ratios and seasonal maximum ARA ($r = -0.50$, $P < 0.05$) (Figure 9), which was evident across stages in 1997 ($r = -0.65$, $P < 0.10$) and across years for mid-succession stands ($r = -0.84$, $P < 0.05$).

Significant relationships between ARA and subcanopy soil chemical characteristics which I did not find for interspace soils were either interpreted as a direct effect of N_2 fixation on soil properties, or a direct effect of soil properties on ARA. I report statistically significant relationships between subcanopy soil parameters and seasonal maximum ARA which are ecologically meaningful. Several of these relationships were specific to the 1998 growing season when water was likely not limiting alder growth and nitrogenase activity.

Although I detected no relationships between soil N parameters and ARA during 1997, % N in O ($r^2 = 0.64$, $P < 0.05$), A ($r^2 = 0.43$, $P = 0.05$) and C ($r^2 = 0.49$, $P < 0.05$) horizon soils correlated positively with ARA across all stands during 1998. Notably, seasonal maximum ARA also correlated positively with interspace soil % N in the O ($r^2 = 0.64$, $P < 0.05$) and C ($r^2 = 0.62$, $P < 0.05$) soil horizons in 1998. ARA was greater in stands where subcanopy soil % P was higher in the O ($r^2 = 0.42$, $P < 0.10$) and A ($r^2 = 0.40$, $P < 0.10$) soil horizons, but these effects were only evident in 1998. I also found positive overall correlations between ARA and soil % C in the O ($r^2 = 0.55$, $P < 0.10$) and C ($r^2 = 0.71$, $P < 0.05$) horizons which were particularly apparent in 1998 ($r^2 = 0.47$, $P < 0.05$ and $r^2 = 0.40$, $P < 0.10$, respectively). These relationships with soil C likely resulted

from inter-correlations between ARA, rates of plant growth, and litterfall carbon contributions.

Nodule biomass and N inputs

Nodule biomass was more variable within than among successional stages, averaging 0.65 ± 0.24, 0.60 ± 0.13, 0.77 ± 0.25 g $nodule_{DWT}$ per soil core beneath alder shrubs from post-fire, mid-succession, and white spruce stages, respectively. For calculations of stand-level N inputs, I used a single average value for nodule biomass per core for all replicate stands within a given successional stage, and assumed nodule biomass was distributed evenly beneath the alder canopy. Stand-level nodule biomass was the product of nodule biomass per canopy, canopy area per shrub, and shrub density for a given replicate stand (Table 4). Because nodule biomass per canopy area was a constant for each successional stage, variation in nodule biomass at the stage level was driven primarily by differences in average canopy areas and shrub densities among stands across stages. This resulted in stand-level nodule biomass estimates of 6.4 ± 0.5, 11.9 ± 1.4, and 22.2 ± 3.3 g nodule m^{-2} for post-fire, mid-succession, and white spruce stages respectively.

Estimates of N inputs (kg N $ha^{-1}yr^{-1}$) averaged across years indicate greatest contribution of N by *A. viridis* to white spruce stands (6.61 ± 1.23), least to early-succession post-fire stands (2.52 ± 0.35), and intermediate to the mid-succession stands (3.24 ± 0.65) ($F_{2,17}$= 6.60, $P < 0.05$) (Figure 10).

Foliar dynamics

Green leaf N concentration varied little from early June through the first week of August. However, as a consequence of lower values after the first week of August, seasonal variation was significant in all successional stages during both study years (all $P < 0.0001$). Seasonal maximum leaf N concentration was greater in white spruce stands (2.86 ± 0.03%) than in mid-succession (2.69 ± 0.05%) and post-fire stands (2.71 ± 0.09%) which did not differ ($F_{1,17} = 5.38$, $P < 0.05$) (Table 7) and there was significant variation among replicate plots within stages ($F_{6,17} = 4.20$, $P < 0.05$). Seasonal maximum leaf %N did not vary between years for any successional stage (Table 8).

Alder in post-fire replicate stands resorbed a larger pool of foliar N (0.68 ± 0.11 g N m^{-2}) compared to plants in mid-succession (0.23 ± 0.07 g N m^{-2}) and white spruce (0.28 ± 0.10 g N m^{-2}) stages, which did not differ ($F_{2,17} = 9.80$, $P < 0.005$) (Table 7). However across successional stages N resorption efficiency did not vary ($F_{2,17} = 2.41$, $P = 0.13$), averaging 27.5 ± 15.6 % across all stages (Table 7). *A. viridis* resorbed a significantly smaller pool of N in 1997 compared to 1998 when averaged across stages ($F_{1,17} = 6.40$, $P < 0.05$), particularly in mid-succession stands ($F_{1,5} = 140.25$, $P < 0.005$) (Table 8). N resorption efficiency in mid-succession was lower in 1997 than 1998 ($F_{1,5} = 39.15$, $P < 0.005$); however, I detected no year effect on N resorption efficiency across successional stages ($F_{2,17} = 2.41$, $P = 0.13$). Averaged across years, alder resorbed a larger pool of foliar N in stands where subcanopy soil P content in the O ($r^2 = 0.22$, $P =$

0.05), A ($r^2 = 0.39$, $P = 0.005$) and C ($r^2 = 0.31$, $P < 0.05$) (Figure 11) horizons and soil % P in the C horizon ($r^2 = 0.25$, $P < 0.05$) were greater.

Leaf %P varied seasonally among post-fire ($F_{5,205} = 5.22$, $P < 0.0005$), mid-succession ($F_{5,197} = 21.95$, $P < 0.0001$) and white spruce ($F_{5,197} = 30.57$, $P < 0.0001$) stages. Overall, seasonal maximum leaf %P was higher in post-fire (0.27 ± 0.04%) than in mid-succession (0.21 ± 0.01%) and white spruce stands (0.23 ± 0.01%) ($F_{2,17} = 13.76$, $P < 0.005$) (Table 7), and variation among replicates within stages also was significant ($F_{6,17} = 11.81$, $P < 0.005$). During 1998, the year of normal precipitation, *A. viridis* produced leaves with a higher seasonal maximum %P compared to 1997 ($F_{1,17} = 17.13$, $P < 0.005$), an effect which was evident in mid-succession ($F_{1,5} = 6.06$, $P = 0.10$) (Table 8) and especially in white spruce stands ($F_{1,5} = 103.29$, $P < 0.05$) (Table 8).

Across all stands, leaf %P varied positively with O horizon P content ($r^2 = 0.17$, $P < 0.10$), A horizon soil % P ($r^2 = 0.18$, $P < 0.10$), total soil N content ($r^2 = 0.22$, $P < 0.05$) and O horizon N content ($r^2 = 0.37$, $P < 0.05$). The positive correlation between leaf % P and O horizon N content was evident in both 1997 ($r^2 = 0.47$, $P < 0.05$) and 1998 ($r^2 = 0.44$, $P < 0.05$).

The pools of P resorbed during senescence were nearly identical among stages, and I detected no significant difference among stages in P resorption efficiency which averaged 15.60 ± 8.80%, 25.53 ± 7.43%, and 32.89 ± 8.01% for post-fire, mid-succession and white spruce stands, respectively (Table 7). Interannual difference was only evident in mid-succession stands, where P resorption pools in 1998 (0.03 ± 0.01) were more than double those in 1997 (0.01 ± 0.01) ($F_{1,5} = 6.67$, $P < 0.10$). However, senescent leaf P

content in mid- and late-succession stands were approximately a third of those in post-fire stands ($F_{2,17} = 8.10$, $P < 0.005$).

Alder produced thicker leaves (higher SLW) in 1998 than in 1997, when averaged across stands ($F_{1,17} = 213.11$, $P < 0.0001$). This difference was evident within post-fire ($F_{1,5} = 49.36$, $P < 0.005$) and white spruce ($F_{1,5} = 88.28$, $P < 0.05$) stands and greatest in mid-succession ($F_{1,5}= 112.68$, $P < 0.0005$) (Figure 12, Table 8). Seasonal maximum SLW was greater in post-fire stands (67.4 ± 39.3 g m^{-2}) than in either mid-succession (39.3 ± 4.4 g m^{-2}) or white spruce (37.1 ± 3.8 g m^{-2}) stands ($F_{2,17} = 270.28$, $P < 0.0001$) (Figure 12, Table 7), and varied little among replicates within stages. Seasonal variation in SLW was not evident in post-fire stands ($F_{5,206} = 1.13$, $P = 0.35$) and minimal in white spruce stands ($F_{5,208} = 3.06$, $P < 0.05$), but pronounced in mid-succession stands ($F_{5,197} = 11.74$, $P < 0.0001$). Near the end of the 1997 growing season I measured a notable increase in SLW in mid-succession stands immediately following the first significant rainfall event (15 mm on August 11) of the dry 1997 growing season.

DISCUSSION

Alder interactions with soil parameters

Across the successional sequence in interior Alaskan upland forests, *A. viridis* displays substantial variation in physiology, growth dynamics, N_2 fixation, and influence on ecosystem function, as it persists through changes in forest community composition and structure. Our data support the following broad statements concerning alder

productivity in each successional stage. Alder growth rates are highest in post-fire stands where light availability is least limiting. During mid succession, where alder grows in the understory of paper birch and trembling aspen, alder stem density, growth rates, and N_2 fixation inputs are suppressed likely due to overstory closure and consequent resource limitation in accordance with the forest growth model proposed by Binkley et al. (2002). On drier south-facing slopes where aspen forms near monospecific stands during early- and mid-successional forest development, *A. viridis* is mostly absent; an effect we attribute to primarily to water limitations (Hogg and Hurdle 1995). In climax succession white spruce stands where *A. viridis* exploits gaps in the overstory canopy alder productivity increases, explaining the substantial increase in green alder stem density with the transition from mid- to late-succession forests (Table 4).

A. viridis alters soil microclimate (Sturm et al. 2005), rates of soil organic matter accumulation, and ecosystem N balance (Rhoades et al. 2001), changes which can lead to modified soil microbial processes (Mack et al. 2001). Shrubs, and N_2-fixing species in particular (Moro et al. 1997), create 'islands' or 'hot spots' of altered soil fertility (Schlesinger et al. 1996, Cross and Schlesinger 1999) such that a species' spatial distribution is mirrored by the spatial distribution of its effect on soil properties (Schlesinger et al. 1996). I identified alder effects on soil properties from relationships between plant parameters and soil characteristics beneath alder canopies which were not found for non-canopy soils. In contrast, relationships between plants traits and soils that were similar for canopy and non-canopy soils were interpreted as stand-level effects on or by alder.

While plant effects on soil properties can diminish or vanish following shifts in species distribution, abundance, and/or vigor, it is also possible that vegetation legacies can persist long after a species is no longer present (Gallardo and Schlesinger 1995, Schlesinger et al. 1996, Seastedt and Adams 2001, Mack et al. 2001). Because alder genets persist by vegetative propagation, and occupy roughly the same spatial location throughout succession, such legacy effects may confuse interpretations of alder influences on, or response to, ecosystem function. Given that *A. viridis* grows rapidly from stump sprouts following fire (personal observation), and appears to spread mainly by vegetative propagation rather than by seed, it is conceivable that such island legacies may persist for centuries, if not decades.

The positive relationship between alder stem density and stand-level total soil C (Figure 5C) across this successional sequence suggests that alder contributes to rates of soil C storage in these forests. This pattern was most pronounced among post-fire stands where increases in stand-level total soil C were related to increasing stem density. Although variation in organic horizon C concentration across all stands was explained principally by successional stage (Table 3), location (canopy vs. non-canopy) was also a significant predictor (Table 5). Together, these data suggest that the collective island effects of alder influence C accumulation rates, and that these effects continue with succession. Similar results have been reported for N_2-fixers in other ecosystems (Johnson 1992, Rhoades et al. 1998).

The influence of alder on ecosystem N balance within and among successional stages differed from that of C because alder N demand relative to soil N availability

appears to vary across succession, and soil N is more subject to movement than is soil C. Among early succession stands, alder stem density was positively correlated with O horizon (Figure 5A) and total soil N stocks; however, no significant "island effect" was detected, despite a non-significant difference between subcanopy (106.1 ± 17.1 g m^{-2}) and interspace (82.6 ± 10.2 g m^{-2}) O horizon N content (Table 6A). Subsurface N transport has been shown to extend 15 m beyond alder canopies, ultimately coalescing into a stand-level N enrichment (Valentine 1990, Rhoades et al. 2001). Given that nitrification rates are highest under alder canopies (Rhoades et al. 2001) or in stands dominated by alders (Kielland et al. in press), a portion of atmospheric N input by alder eventually ends up as nitrate. Leaching of nitrate into deeper horizons may persist into mid succession, where I detected a positive correlation between alder stem density and C horizon soil % N. A positive relationship between alder stem density and O horizon % N was found for both canopy and non-canopy soils in mid-succession stands. While these patterns may have indicated stand N influences on alder growth, I suspect that island N effects remain but were difficult to detect. During mid succession where alder productivity appeared to be suppressed, alder N demand may exceed N_2 fixation capacity, given that subcanopy A horizon N content (43.4 ± 4.6 g N m^{-2}) was significantly lower than that of non-canopy soils (59.9 ± 8.2 g N m^{-2}) (Table 6B).

Across all successional stages, organic soil % N averaged 1.17 ± 0.05% under alder and 1.03 ± 0.05% in interspace soils (Table 5); however, this difference was most pronounced in white spruce stands (Table 6C). In white spruce stands where continuous moss cover is interrupted by islands of high-N alder litterfall, soils under alder exhibited

18% less O horizon mass, but had 27% higher N concentration relative to non-canopy soils (Table 6C). Greater forest floor N concentrations and turnover rates under alder relative to patches comprised of moss and coniferous litter likely account for these patterns (Van Cleve et al. 1983). It is worth noting that my %N values for non-canopy O horizon soils (Table 5), sampled only 2 m beyond the alder canopy were greater than those determined previously for these same late succession stands (http://www.lter.uaf.edu), suggesting that the immediate influence of alder may extend well beyond the canopy perimeter.

Alnus can lead to soil acidification as a byproduct of increased nitrification rates (Van Migroet and Cole 1984, Binkley and Sollins 1990, Rhoades et al. 2001). I detected subcanopy soil acidification only in post-fire stands, where pH beneath alder canopies was reduced by 0.1 to 0.5 units throughout the soil profile relative to non-canopy soils (Table 6A). However, it is conceivable that legacies of soil acidification from post-fire stands may have persisted into mid- and late-succession stands within progressively deeper soil horizons. This was suggested by the inverse relationship that I found between alder stem density and soil pH in both A and C mineral horizons in mid-succession stands and within C mineral horizon soils in white spruce stands.

Similar to patterns for other successional forest sequences forests (Wardle et al. 2004), I found a significant decline in total soil P within the top 20 cm from post-fire (79 ± 2 g P m^{-2}), to mid-succession (54 ± 3 g P m^{-2}) to white spruce (44 ± 3 g P m^{-2}) stands (Figure 4). Given the high P requirement of N_2-fixing plants (Wall et al. 2000, Huss-Danell et al. 2002, Vitousek et al. 2002), I predicted strong effects of alder on, and in

response to, soil P across this successional sequence. In post-fire stands, where P availability is highest due to mobilization from fire (Valentine et al. 2006), I found no significant effects of alder on %P or P content of any soil horizon. Uliassi and Ruess (2002) found significant increases in nodulation and N_2 fixation rates following P fertilization in *A. tenuifolia* growing in early and mid-succession floodplain stands along the Tanana River, where most soil P is bound as insoluble inorganic complexes (Marion et al.1993). I might expect similar responses in *A. viridis* to P fertilization in mid- and late-succession upland stands, where C horizon P content was 18% and 24% lower in canopy soils relative to non-canopy soils in white spruce and mid-succession stands, respectively (Tables 6A and 6B). Although I believe soil water was the primary factor limiting alder growth and N_2 fixation rates in upland stands, alder-P relations and the effects of soil water on these relations remain important, but poorly-studied, topics.

N_2 fixation

Plant phenology (julian day) explained the largest percent of variation in N_2 fixation rates among sampling periods across successional stages. Similar results have been reported for *A. tenuifolia* growing in interior Alaskan floodplain forests (Uliassi and Ruess 2002, Anderson et al. in prep) and *A. incana* in northern Sweden (Huss-Danell et al. 1991); these findings most simply reflect that N_2 fixation closely tracks plant growth and N demand within the growing season. My most parsimonious model included a non-linear response to plant phenology (indexed by Julian day) and an independent, linear

response to soil temperature. However, this combined model explained only 23% of the variation in N_2 fixation rates across successional stages, and was not improved by inclusion of leaf chemical parameters, such as N, P, or N:P ratios. This low explanatory power over field N_2 fixation rates is not uncommon (Uliassi and Ruess 2002, Anderson et al. 2004, Anderson et al. in prep), and probably results from a combination of ecophysiological factors and sampling limitations. In particular, I suspect that soil moisture data for each field ARA measurement would have improved my models substantially. The inclusion of nodules of different ages, or perhaps even dead nodules (Zitzer and Dawson 1989), and inherent differences in the condition, age, and growth rates of roots to which nodule clusters were attached may have also contributed to the high variability among my ARA measurements. In addition, the reduction ratio of C_2H_2 to N_2 is known to vary by over an order of magnitude in both *A. viridis* and *A. tenuifolia* (Anderson et al. 2004), limiting the utility of ARA as a reliable index of N_2-fixation rates. Another factor influencing nodule activity may be the differences in genetic structure of *Frankia* haplotypes within nodule clusters at the plant, stand, and landscape scales (Anderson et al. in prep).

When data were pooled across all stands, seasonal maximum rates of N_2 fixation were slightly lower during the dry year of 1997 (5.4 ± 0.5 μmol C_2H_4 g $nodule_{DWT}^{-1}$ hr^{-1}) compared to 1998 (6.6 ± 0.6 μmol C_2H_4 g $nodule_{DWT}^{-1}$ hr^{-1}), a year of relatively normal precipitation. This non-significant result was largely driven by higher N_2 fixation rates in mid-succession stands (+76%), and there were non-significant increases in early (+7%) and late (+7%) succession during the wetter year (Figure 8). My measured peak rates

were less than those measured by Anderson et al. (2004), who reported averages across these same stands ranging from 7.0 to 16.3 μmol C_2H_4 g $nodule_{DWT}^{-1}$ hr^{-1} during a later, normal-precipitation year. Given that their study was not designed specifically to capture seasonal maximum rates, the differences between the two studies were likely conservative. Thus, it appears that I may not have captured the N_2 fixation potential of *A. viridis* in either 1997, as a direct consequence of drought, or in 1998, perhaps as a result of resource allocation to growth recovery following disturbance the previous year (Ruess et al. 2006).

One of my most striking results was the lack of variation in maximum N_2 fixation rates across successional stages, which averaged 6.8 ± 1.3, 6.5 ± 1.1, and 6.5 ± 1.1 μmol C_2H_4 g $nodule_{DWT}^{-1}$ hr^{-1} in early-, mid-, and late-succession stages, respectively, during 1998 (Figure 8). This contrasts with studies of *A. tenuifolia* which showed a pronounced decline in fixation rates with the progression from early (25.0 ± 8.0 μmol C_2H_4 g $nodule_{DWT}^{-1}$ hr^{-1}), to mid (17.5 ± 3.1 μmol C_2H_4 g $nodule_{DWT}^{-1}$ hr^{-1}) (Uliassi and Ruess 2002), to late (10.8 ± 1.3 μmol C_2H_4 g $nodule_{DWT}^{-1}$ hr^{-1}) succession stands (Uliassi and Ruess 2002, Anderson et al. 2004). I have already mentioned two factors that may contribute to the absence of a successional pattern in ARA. The first is drought, which may have masked otherwise greater differences among stages. The second factor is the reduction ratio of C_2H_2 to N_2, which Anderson et al. (2004) found to be inversely correlated with N_2 fixation rates as determined by $^{15}N_2$ uptake. This means that if there were higher rates of N_2 fixation in early succession stands, as I initially hypothesized because of high levels of light and perhaps higher soil P, these might go undetected as the

inhibition of N_2 reduction by C_2H_2 declines at high rates of electron flux through the nitrogenase complex (Anderson et al. 2004). Finally, lower potential relative growth rates, plant N demand, and ARA in *A. viridis* relative to *A. tenuifolia* (Ruess, unpublished data) may also contribute to the differences between these two species and landscapes. If water is less limiting in floodplain relative to upland forests, *A. tenuifolia* in early succession floodplain stands may be growing closer to its maximum potential, and therefore be much more sensitive to other growth limitations later in succession compared with the more slow-growing *A. viridis*.

N_2 fixation and climate sensitivity

Across all stands *A. viridis* produced thinner leaves (Figure 12) during the dry year, which likely translated to reduced litterfall inputs of C, N and P in the low precipitation year. Given the importance of *A. viridis* on soil properties as mediated through litterfall inputs, I predict that periodic reductions of alder litterfall inputs to subcanopy soils in response to water limitation could have significant implications for ecosystem-level N cycling dynamics (Knops et al. 2002).

It seems likely that my result of diminished foliar P concentration in the dry year was related to reduced photosynthesis and associated diminished soil nutrient uptake in response to drought (Minoletti and Boerner 2004, Wright et al. 2001). Drought-stress has also been shown to negatively affect the ability of alder to allocate photosynthate to other physiological processes necessary for maintaining plant nutrient balance including C

supply to *Frankia* (Lundquist 2005), ectomycorrhizae (Rygiewicz and Andersen 1994), and the formation and maintenance of both fine roots (Ruess et al. 2003) and cluster roots (Ruess et al. 2003, Shane and Lambers 2005). Support of ectomycorrhizal symbionts may be particularly important for maintaining optimal N to P balance in N_2-fixing woody plants growing under both P-limiting and water-limiting conditions (Querejeta et al. 2003).

The drought of 1997 had the most severe effects on alder in mid-succession stands where, as previously described, N_2 fixation rates and leaf thickness were significantly reduced relative to values in 1998 (Table 8). Notably, my finding of thinner leaves in this and other successional stages (Figure 12) during the drought year (Table 7) has not been previously documented (Reich, personal communication). Furthermore, it was interesting to note that alder in mid-succession stands responded dramatically to a late growing season precipitation event which ended the drought of 1997. Immediately following 15 mm of rainfall on 11 August, alders in mid-succession stands produced a cohort of leaves that were 26% thicker (39 g m^{-2}) compared to the previous cohort sample in July (31 g m^{-2}). Interestingly, resorption of foliar N and P from this younger leaf cohort during fall was significantly lower than values recorded in mid-succession stands in 1998 (or in the other two stages in 1997) (Table 8). I believe this resulted from prolonged leaf retention in order to extend the photosynthetic life of leaves. Tateno (2003) argued that for non-N_2-fixing plants, the benefits afforded by N resorption in fall outweigh the potential C gains of retaining leaves longer in the growing season, but speculated that in N_2-fixing plants, such advantages to N balance may not be necessary.

But this argument overlooks the inherently high P demands in N_2-fixing species, and their capacity for efficient P resorption. For example, working in interior Alaskan upland forests, Chapin and Kedrowski (1983) reported less N resorption for *A. viridis* relative to *Betula papyrifera* (61% vs. 75%, respectively) but greater P resorption in *A. viridis* (81% vs. 44%, respectively). Uliassi and Ruess (2002) showed that P resorption efficiency in *A. tenuifolia* growing in early succession floodplain stands was reduced from 51.4% to 10.5% in response to P fertilization. For reasons I can't explain, my values for both N (27%) and P (24%) resorption efficiency (averaged across all stands for both 1997 and 1998) were considerably less than have been measured previously (Chapin and Kedrowski 1983). Given that alders typically retain leaves longer than other deciduous woody plants in interior Alaska, a flexible strategy of prolonging C gain to support *Frankia*, but also ectomycorrhizae for the acquisition of P (Read et al. 2004), may be an important adaptation for maintaining C and nutrient balance under variable climatic conditions.

N inputs

My estimates of annual N inputs by *A. viridis* to upland stands of the Bonanza Creek Experimental Forest (2.5 – 6.6 kg $ha^{-1}yr^{-1}$) (Figure 10) were substantially less than those reported by Uliassi and Ruess (2002) for *A. tenuifolia* in early- and mid-successional floodplain forests along the Tanana River (38 – 59 kg·ha^{-1}·yr). Differences between species in N inputs were the product of lower *A. viridis* plant density (Table 4),

nodule biomass, and ARA-assessed N_2 fixation relative to *A. tenuifolia*. However, several uncertainties in my estimates suggest that my values underestimate the actual potential for N_2 fixation inputs by *A. viridis* to these upland forests. First, as mentioned above, I believe N_2 fixation was suppressed by drought in both study years. Secondly, I suspect I may have underestimated nodule biomass, given my low sample size and the inherent variability in the spatial distribution of nodules (personal observation). My calculations assumed that nodule biomass was distributed evenly beneath alder canopies; however, when collecting nodules for acetylene reduction assays, I often observed declines in nodule biomass with distance from the main stem, with numerous nodule "hot-spots" throughout the sub-canopy. For example, nodule biomass ranged from 0.01 g to 6.84 g per 15.24 cm diameter soil core, averaging 0.75 ± 0.15 g (n = 59, CV = 19.4%). Thirdly, as discussed by Anderson et al. (2004) there may be a number of errors propagated by the ARA method that mask actual fixation rates at the nodule level. Based on a greenhouse study where *A. tenuifolia* exhibited approximately three times higher rates of acetylene reduction than *A. viridis* when grown under controlled conditions (Ruess, unpublished data), I had hypothesized that these apparent species differences would translate to the field. A recent study by Anderson et al. (in prep.) also reported higher N_2 fixation rates (when measured during peak periods using an *in situ* $^{15}N_2$ uptake method) by *A. tenuifolia* (69.4 ± 13.8 μmol N g nodule^{-1} hr^{-1}) growing in early-succession floodplain stands compared with *A. viridis* (39.2 ± 4.7 μmol N g nodule^{-1} hr^{-1}) in the same post-fire stands visited in the present study,. Although I believe these differences translate to contrasting N inputs for upland and floodplain forests, better estimates of

nodule biomass and activity are necessary to understand how the apparent differences in growth capacity and N_2 fixation traits between the two species scale to ecosystem-level N balance.

Ignoring for the moment the uncertainties in my N_2 fixation inputs reviewed above, my data indicate that *A. viridis* contributed more N to late succession white spruce stands (6.6 ± 1.2 kg ha^{-1} yr^{-1}) than to earlier post-fire (2.5 ± 0.4 kg ha^{-1} yr^{-1}) and mid-succession (3.2 ± 0.7 kg ha^{-1} yr^{-1}) stands (Figure 10). This increase resulted primarily from greater alder abundance in late (290 ± 62 shrubs ha^{-1}) compared to early (90 ± 10 shrubs ha^{-1}) and mid (179 ± 30 shrubs ha^{-1}) successional stages (Table 4). This pattern contradicts both predictions and observations of declining N inputs as a function of decreased abundance of N_2-fixing vascular plants during forest succession (Vitousek and Howarth 1991, Chapin et al. 1994, Vitousek and Field 1999, Vitousek et al. 2002). Rastetter et al. (2001) developed an ecosystem model for temperate forests based on plant resource optimization explaining this general restriction of N_2-fixing vascular plants to early succession. Factors contributing to sustained activity of N_2 fixers in early succession included an open canopy, low soil N levels, and a soil volume well-exploited by roots, while interspecific competition and the costs of N_2 fixation vs. uptake were important factors explaining the loss of N_2-fixing plants from late succession. Interestingly, the factors identified by Rastetter et al. (2001) as those favoring N_2 fixers are all characteristics of my late-succession upland white spruce stands. The capacity of *A. viridis* to propagate vegetatively allows it to persist during the early development of white spruce dominance, where it creates and maintains canopy caps. Interspecific

competition is reduced due to the inability of hardwood species to invade the near continuous moss ground cover, and the tendency of white spruce to self thin as it ages. The result is that alder stem density increases substantially during the transition from mid to late succession, resulting in moderate rates of N input that may be sustained for a century.

Recent studies from both tropical (Matzek and Vitousek 2003) and boreal (DeLuca et al. 2002, Zackrisson et al. 2004) forests show that the persistence of N_2-fixing non-vascular plants can maintain and even increase N_2 fixation inputs during late successional stages. In boreal forests, associations between common feather mosses and cyanobacteria, including *Nostoc*, may result in N input that may be low, but persistent for over centuries. Working across a fire chronosequence in northern Sweden, Zackrisson et al. (2004) estimated N_2 fixation inputs by *Pleurozium schreberi* ranging from < 0.5 kg N ha^{-1} yr^{-1} in early succession stands (25-80 years post fire) to between 1.0 and 2.0 kg N ha^{-1} yr^{-1} for late succession stands (> 200 years post fire). This linear increase in acetylene reduction activity with successional time was a function of the presence (2 to > 70% ground cover across this chronosequence) and activity of *Pleurozium schreberi*. Acetylene reduction activity was unaffected by *Hylocomium splendens* which was another feather moss found in much lower abundance (<5% cover across all stands in the Swedish successional chronosequence), despite evidence that per gram tissue, *Hylocomium splendens* fixes N_2 at rates comparable with those reported for *Pleurozium schreberi* (DeLuca, personal communication). Characterization of moss communities at the Bonanza Creek LTER stands has found *Pleurozium schreberi* in relatively low

abundance, averaging <3% ground cover in upland and floodplain white spruce stands, and even less so in earlier stages (Willsrud 1997). *Hylocomium splendens* constituted 83% and 62% of moss cover in upland and floodplain white spruce stands, respectively; however, total moss cover averaged only 33% and 39% in these stages (Willsrud 1997), far less than that found in the Swedish forests mentioned above. However, given the comparatively low coverage of feather mosses in white spruce stands, coupled with relatively arid conditions that may render mosses dormant for much of the growing season, I suggest that N inputs by *A. viridis* were well over an order of magnitude greater than those of feather mosses.

CONCLUSIONS

I provide evidence that *A. viridis* was a modest but significant contributor of fixed N to this post-fire upland chronosequence and that N inputs were greatest in late succession spruce stands. To my knowledge I am the first to estimate annual N_2 fixation inputs directly by *A. viridis*, and my study represents the first report of an increase in N_2-fixation inputs across a successional sequence by any vascular plant species. I attribute the increase in total soil N from mid- to late-succession stands to greater alder stem density in late succession stands, since I did not detect changes in N_2 fixation rates or nodule biomass across the chronosequence.

My finding of high alder stem density in late succession stands contradicts theoretical models which predict diminishing N_2 fixer abundance over successional time in response to increasing competition for limiting resources (Vitousek and Howarth 1991,

Chapin et al. 1994, Vitousek and Field 1999, Rastetter et al. 2001, Vitousek et al. 2002). In agreement with earlier studies, I report some evidence that alder was both light- and P-limited. However, my results strongly suggest that water availability was the primary factor limiting alder growth on both annual and successional timescales. For example, I found that while response to low water availability was most pronounced in the mid-succession stage, *A. viridis* was less productive in a low precipitation year throughout the chronosequence. I attribute the near absence of alder from aspen-dominated mid-succession stands to competitive exclusion related to water limitation and suggest that the density of green alder could be reduced within other mid succession stands if the current trend of warming and drying throughout interior Alaska (Barber et al. 2000) continues. Given the substantial N inputs by *A. viridis* to late succession stands, failure to persist through middle-succession stands could profoundly influence the N economy of this vegetation chronosequence.

Studies of modern shrub expansion in the arctic tundra have focused on potential alterations to hydrological and energy balances (Chapin et al. 2000, Sturm et al. 2001, Tape et al. 2006). For example, greater snow accumulation promoted by large shrubs has been found to alter surface albedo and stimulate a positive feedback loop associating the insulating effect of greater snow accumulation around shrubs with warmer temperatures, increased soil microbial activity (summer and winter) and thus enhanced nutrient availability (Sturm 2001). There is also strong evidence that *A. viridis* stimulates the N economy (Vogel and Gower 1998, Rhoades et al. 2001, Densmore 2005) and hence growth of associated species. For instance, alder stimulation of plant available soil N

may partially explain the observed 'halos' of dwarf birch and willow surrounding alder clumps throughout the north slope of the Brooks Range (Tape et al. 2006). Despite evidence from this and other studies that *A. viridis* (the dominant component of shrub expansion), stimulates proximal and stand level soil N in boreal and arctic ecosystems (Vogel and Gower 1998, Rhoades et al. 2001), the N_2-fixing capacity of alder has been overlooked by most studies discussing arctic shrub expansion. Given the pronounced effects of alder on ecosystem structure and function throughout western and northern Alaska during the last significant shrub expansion which took place during the mid-Holocene (Anderson and Brubaker 1994, Oswald et al. 1999, Hu et al. 2001), it is reasonable to assume that significant N inputs to tundra may substantially alter similar properties of these systems.

Large-scale shifts in primary production and N cycling associated with alder invasion into areas occupied by tussock tundra could also modify ecosystem C budgets (McGuire et al. 2002). For example, long term experimental N fertilization of tundra plots near Toolik Lake in arctic Alaska led to loss of C from deep soil horizons, mediated through microbially-stimulated decomposition that exceeded increases in NPP (Mack et al. 2004). Although I found no evidence for loss of deep soil C beneath alder canopies in boreal upland forests, it would be interesting to examine whether declines in sub-surface soil C stocks have occurred in arctic landscapes where alder has expanded most dramatically in the last several decades (Tape et al. 2006).

Recent shrub expansion throughout western (Silapaswan et al. 2001) and northern Alaska has correlated with recent climatic warming; however, it has been suggested that

shrub range expansion may have been initiated over a century ago (Tape et al. 2006), prior to the warming trend of the last 30 years (Serezze et al. 2000, Keyser 2000, Hinzman 2000). The current explanation involves an increase in soil nutrient availability brought on by elevated winter soil temperatures resulting from increased snowpack (Sturm et al. 2005). Support for this hypothesis comes from increases in shrub density within the long-term N fertilization plots at Toolik Lake (Shaver et al. 2001). However, my observations regarding the sensitivity of *A. viridis* to water stress, and evidence that alder expansion during the Holocene was related to warmer temperatures and increased effective moisture (Hu et al. 2001, Mann et al. 2002), suggest that modern alder expansion may also be influenced by soil moisture regime.

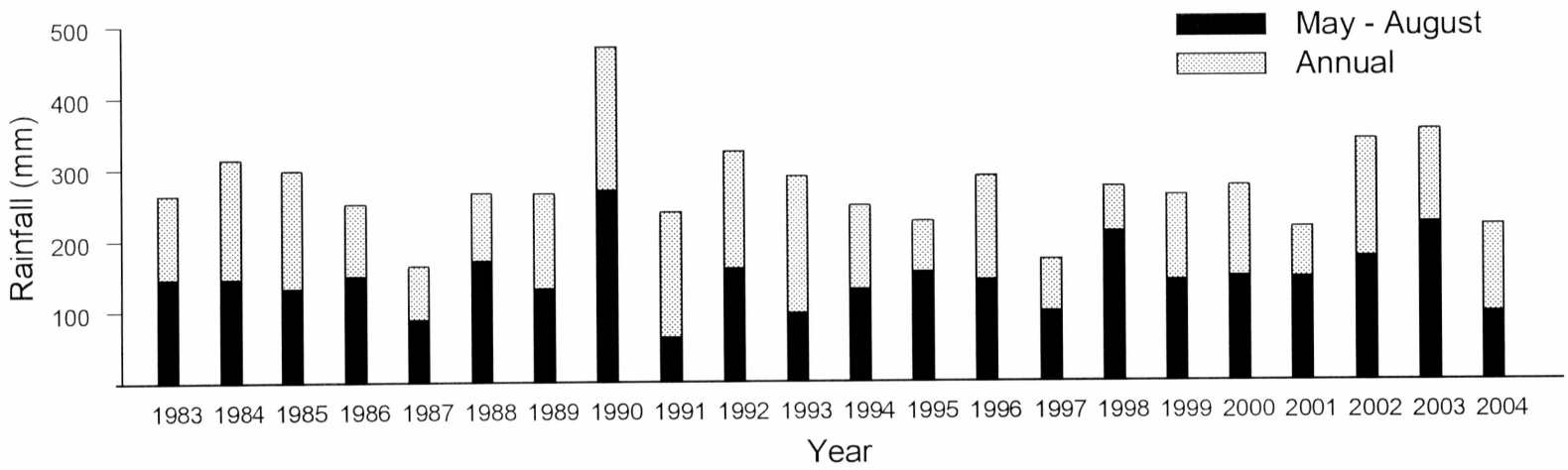


FIGURE 1. Total annual and summer precipitation in Fairbanks, Alaska from 1983-2004. Data source: Geophysical Institute on-line climate database, University of Alaska Fairbanks.

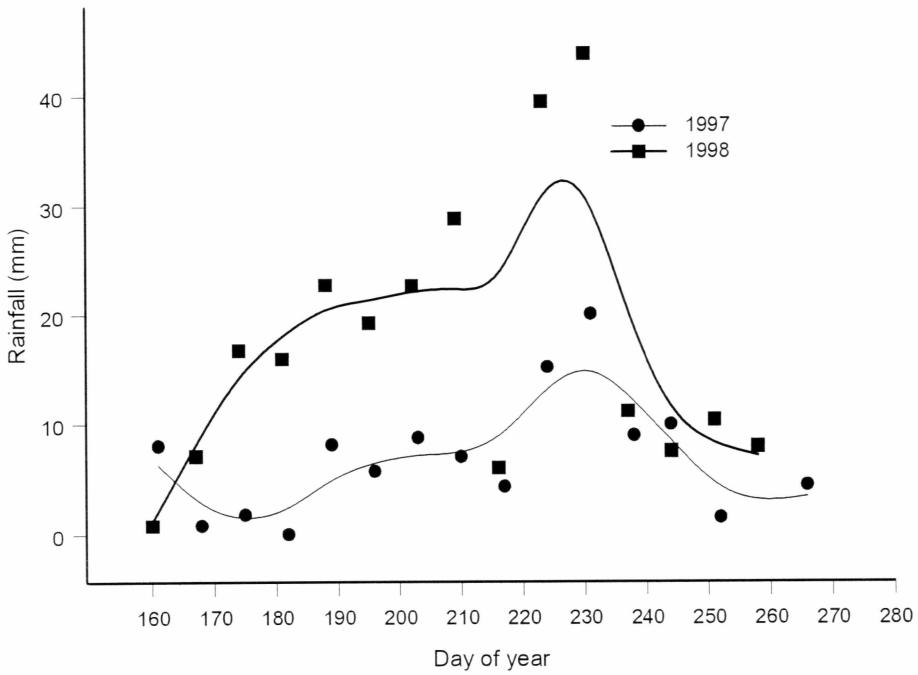


FIGURE 2. Seasonal rainfall patterns for 1997 and 1998 at the Bonanza Creek Experimental Forest. Data source: Bonanza Creek LTER on-line climate database.

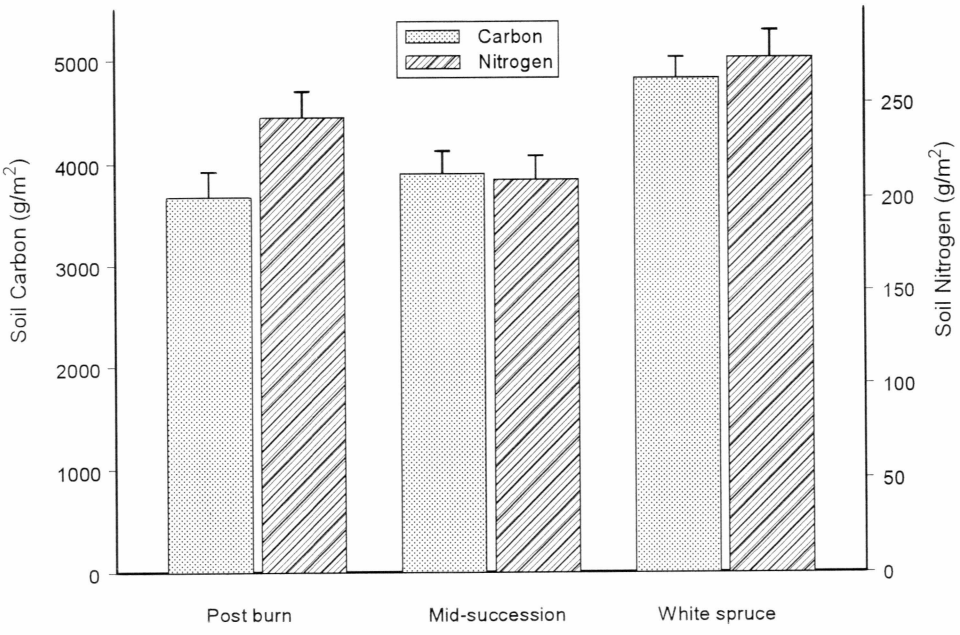


FIGURE 3. Total soil nitrogen and carbon content (to 20 cm soil depth) in upland forest stages within the Bonanza Creek Experimental Forest. Letters indicate differences between stages at $P < 0.05$. Values are means ± 1 SE (N = 34).

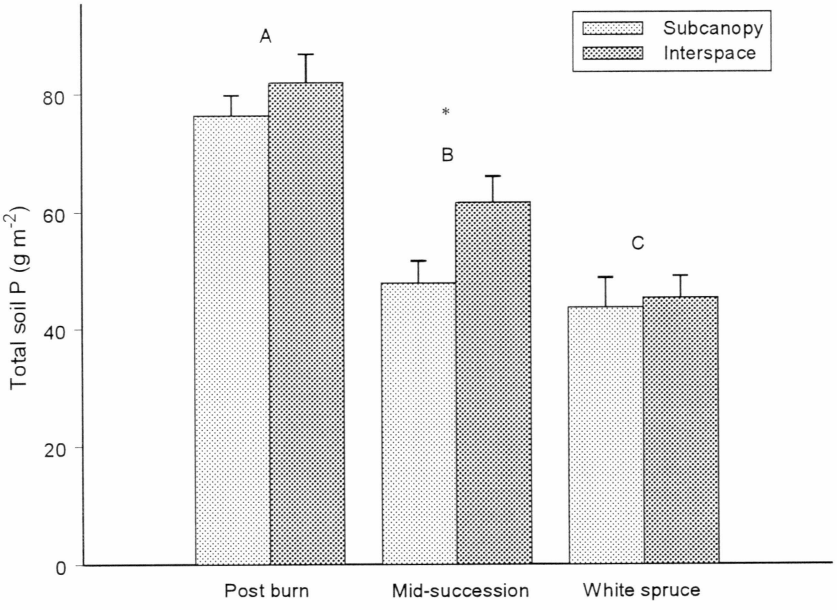
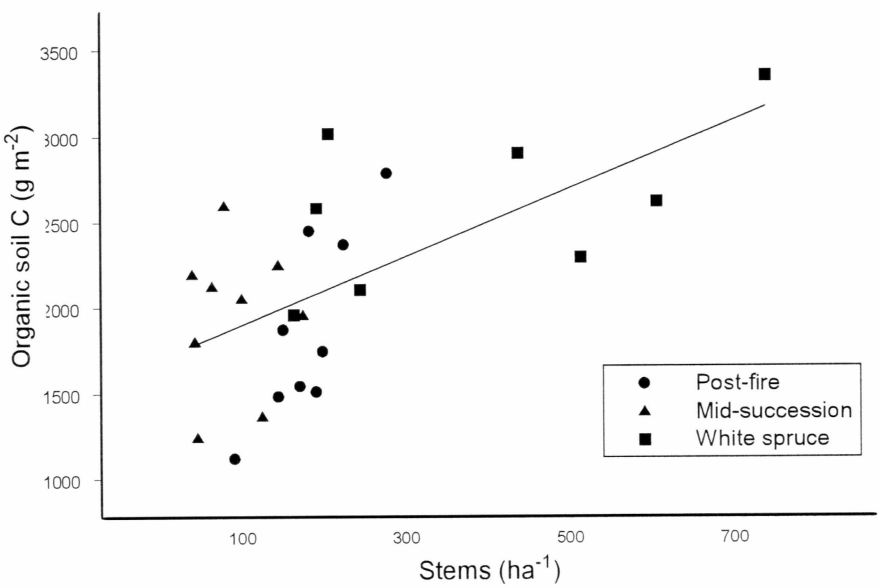
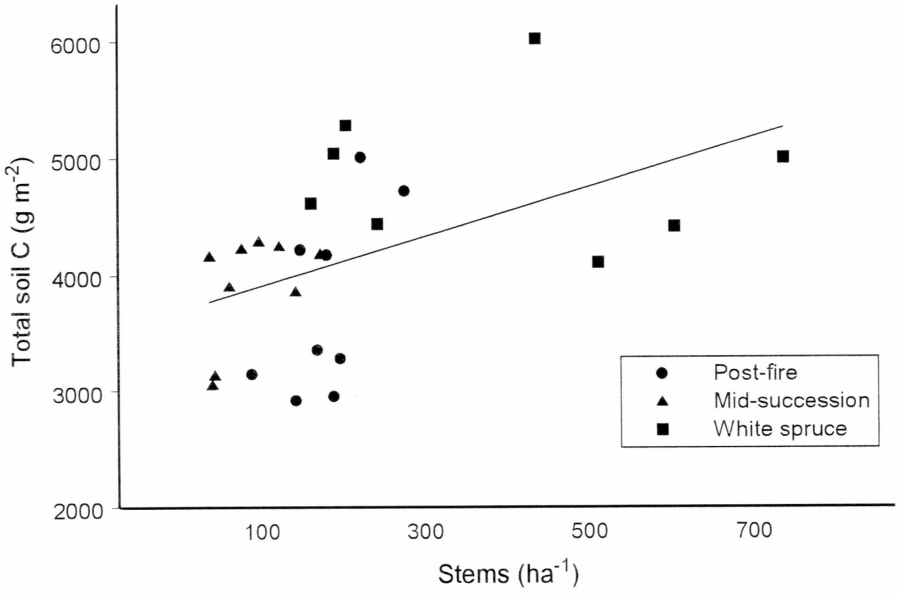


FIGURE 4. Total phosphorus content (to 20cm soil depth) in alder subcanopy and interspace soils in upland forest stages within the Bonanza Creek Experimental Forest. Letters indicate differences between stages, and *s indicate differences between soils under alder canopies compared to interspace soils at $P < 0.05$. Values are means ± 1 SE (N = 17).



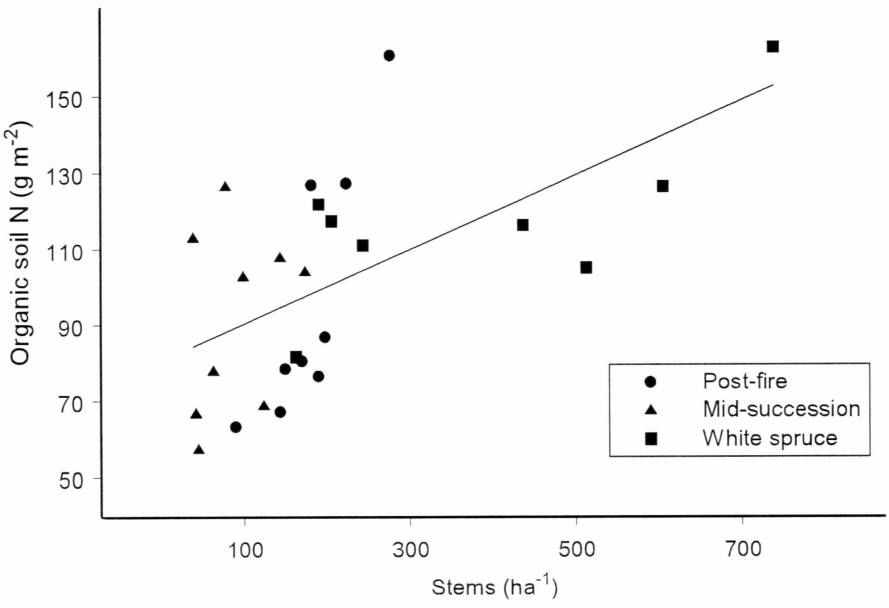
A.

FIGURE 5. Relationships between *A. viridis* stem density and (A) organic soil carbon content (Y = 2.00X + 16.99, $r^2 = 0.37$, $P < 0.005$), (B) total soil carbon content (to 20 cm soil depth) (Y = 2.10X + 3698, $r^2 = 0.22$, $P < 0.05$), and (C) organic soil nitrogen content (Y = 0.10X + 80.39, $r^2 = 0.35$, $P < 0.005$) across upland forest stages within the Bonanza Creek Experimental Forest. Values are means (N = 5) for soil parameters.



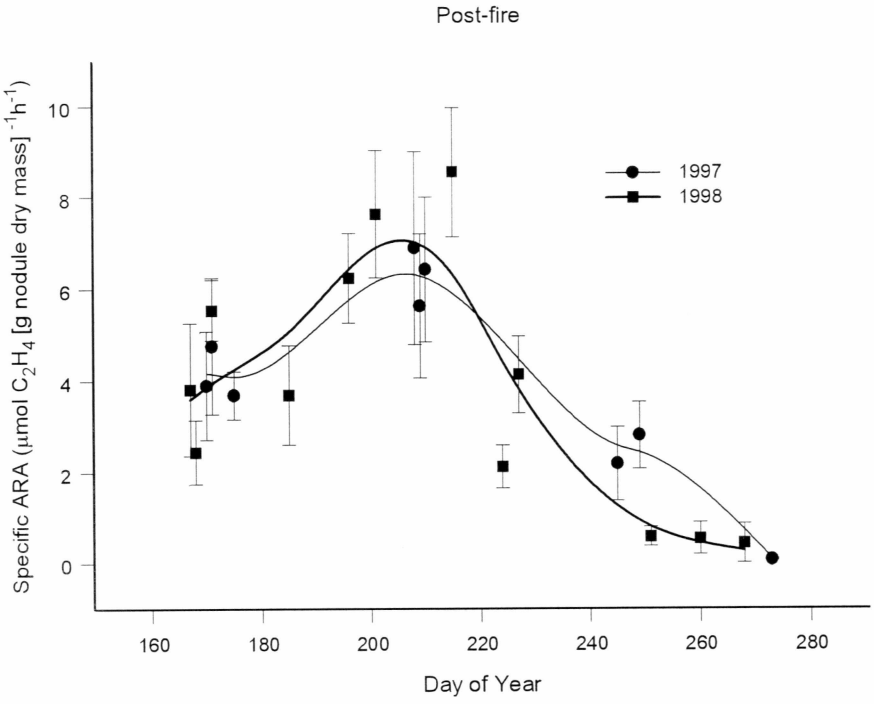
B.

FIGURE 5 CONTINUED. Relationships between *A. viridis* stem density and (A) organic soil carbon content ($Y = 2.00X + 16.99$, $r^2 = 0.37$, $P < 0.005$), (B) total soil carbon content (to 20 cm soil depth) ($Y = 2.10X + 3698$, $r^2 = 0.22$, $P < 0.05$), and (C) organic soil nitrogen content ($Y = 0.10X + 80.39$, $r^2 = 0.35$, $P < 0.005$) across upland forest stages within the Bonanza Creek Experimental Forest. Values are means (N = 5) for soil parameters.



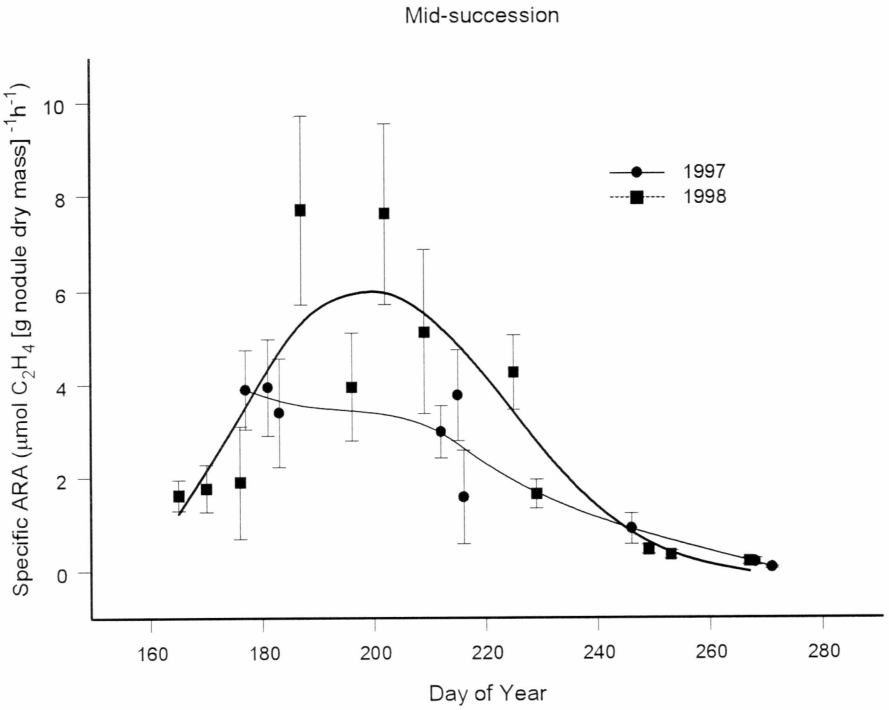
C.

FIGURE 5 CONTINUED. Relationships between *A. viridis* stem density and (A) organic soil carbon content ($Y = 2.00X + 16.99$, $r^2 = 0.37$, $P < 0.005$), (B) total soil carbon content (to 20 cm soil depth) ($Y = 2.10X + 3698$, $r^2 = 0.22$, $P < 0.05$), and (C) organic soil nitrogen content ($Y = 0.10X + 80.39$, $r^2 = 0.35$, $P < 0.005$) across upland forest stages within the Bonanza Creek Experimental Forest. Values are means (N = 5) for soil parameters.



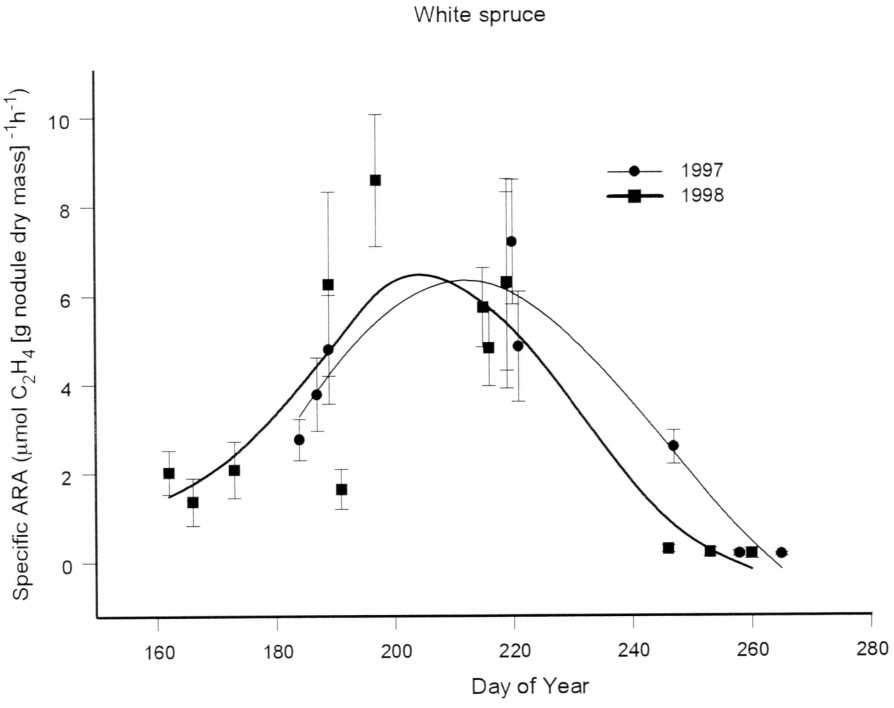
A.

FIGURE 6. Seasonal patterns of acetylene reduction activity (ARA) by *A. viridis* during study years for (A) post-fire, (B) mid-succession and (C) white spruce upland forest stages within the Bonanza Creek Experimental Forest. Curves represent spline interpolation functions through all data points for each year. Values are means ± 1 SE (N = 10).



B.

FIGURE 6 CONTINUED. Seasonal patterns of acetylene reduction activity (ARA) by *A. viridis* during study years for (A) post-fire, (B) mid-succession and (C) white spruce upland forest stages within the Bonanza Creek Experimental Forest. Curves represent spline interpolation functions through all data points for each year. Values are means ± 1 SE (N = 10).



C.

FIGURE 6 CONTINUED. Seasonal patterns of acetylene reduction activity (ARA) by *A. viridis* during study years for (A) post-fire, (B) mid-succession and (C) white spruce upland forest stages within the Bonanza Creek Experimental Forest. Curves represent spline interpolation functions through all data points for each year. Values are means ± 1 SE (N = 10).

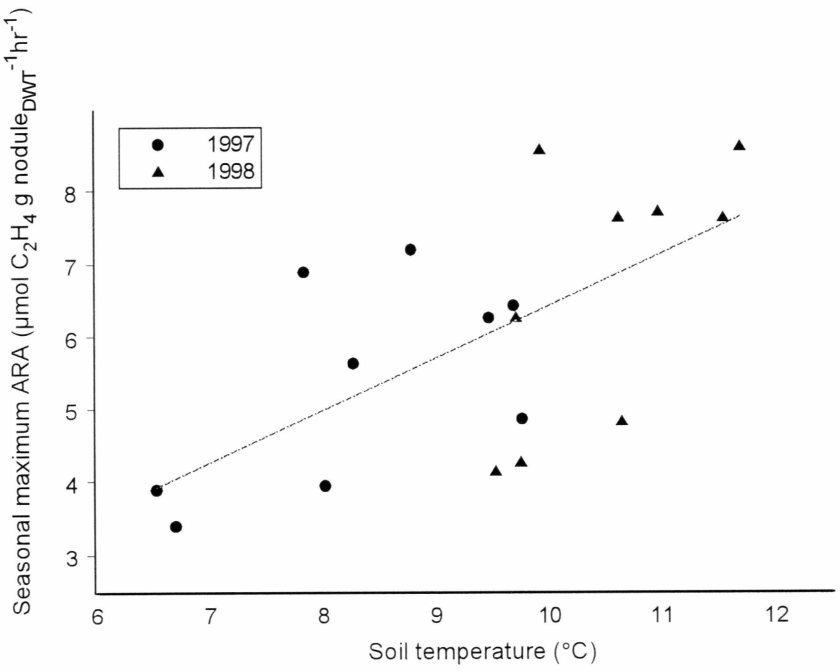


FIGURE 7. Relationship between seasonal maximum rates of ARA by *A. viridis* and concurrent soil temperature across upland forest stages within the Bonanza Creek Experimental Forest (Y = 0.72X - 0.80, $r^2 = 0.40$, $P < 0.005$). Values are means for ARA (N = 10).

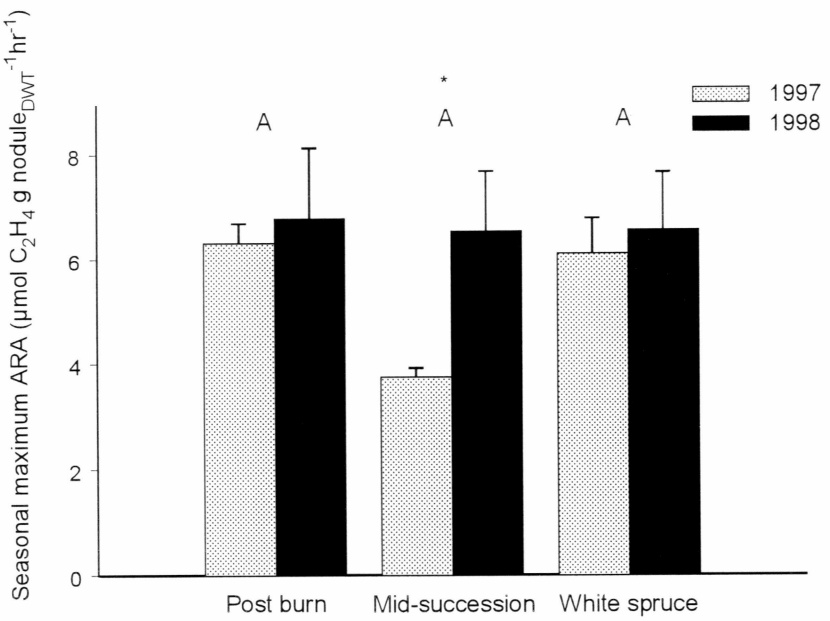


FIGURE 8. Seasonal maximum rates of acetylene reduction activity (ARA) by *A. viridis* in upland forest stages within the Bonanza Creek Experimental Forest. Letters indicate differences between stages and *s indicate differences between years at $P < 0.05$. Values are means ± 1 SE (N = 30).

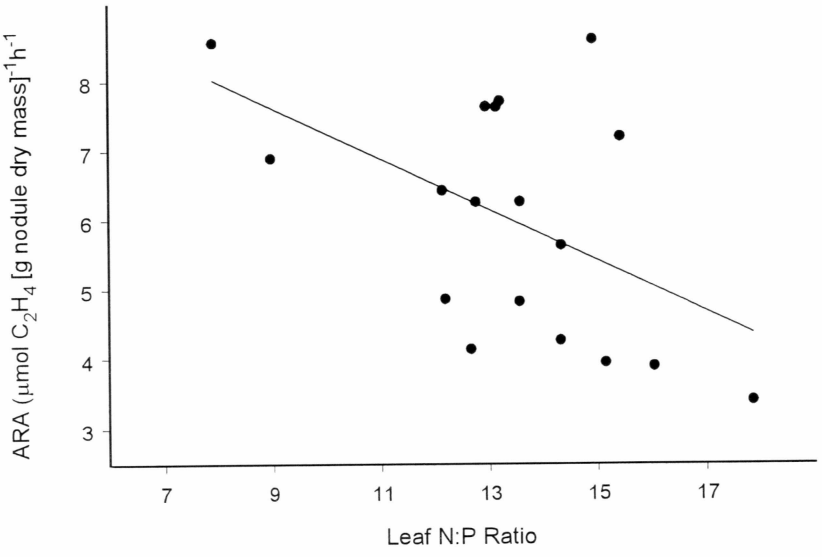


FIGURE 9. Relationship between seasonal maximum rates of ARA by *A. viridis* and foliar N:P ratio across upland forest stages within the Bonanza Creek Experimental Forest (Y = 0.37X – 10.91, r = -0.50, $P < 0.05$). Values are means for ARA (N = 10).

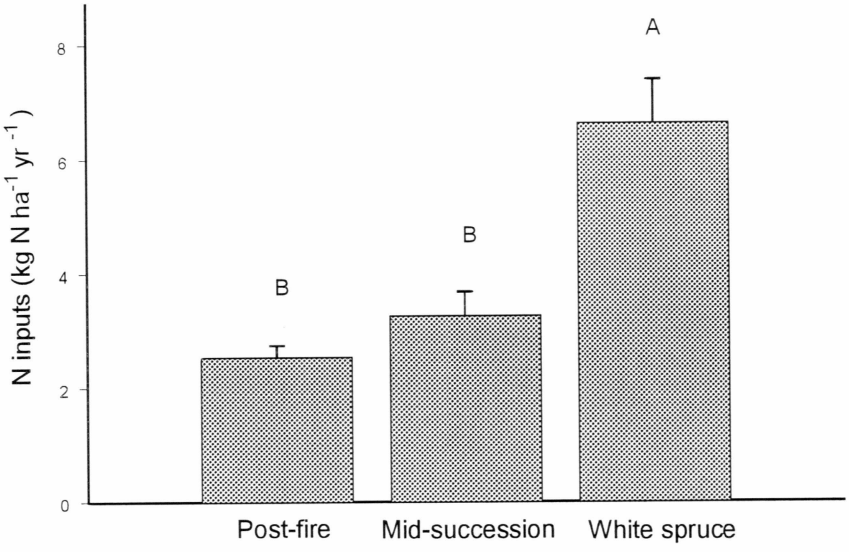


FIGURE 10. Nitrogen inputs by *A. viridis* in upland forest stages within the Bonanza Creek Experimental Forest. Letters indicate differences between stages at $P < 0.05$. Values are means ± 1 SE (N = 2).

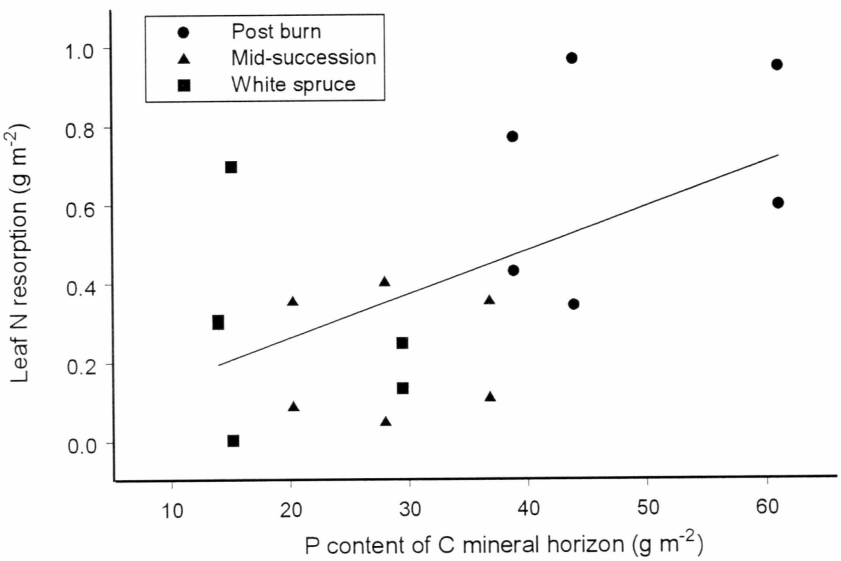


FIGURE 11. Relationship between foliar N resorption by and soil phosphorus content in C horizon soil P content in upland forest stands for two years within the Bonanza Creek Experimental Forest ($Y = 0.01X + 0.04$, $r^2 = 0.55$, $P < 0.05$).

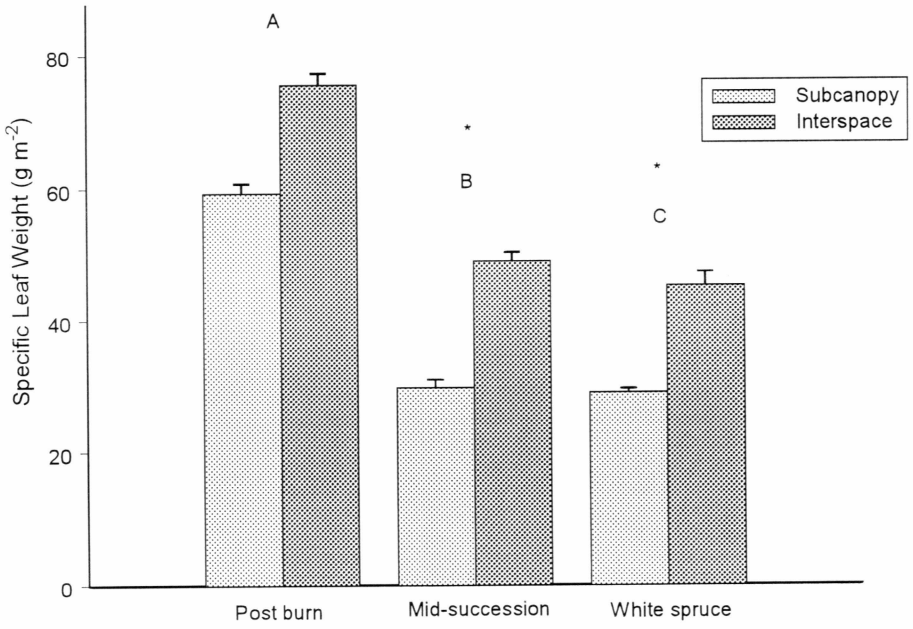


FIGURE 12. Specific leaf weight (SLW) of *A. viridis* in upland forest stages within Bonanza Creek Experimental Forest. Letters indicate differences between stages and *s indicate differences between years at $P < 0.05$. Values are means ± 1 SE (N = 30).

TABLE 1. Sampling periods for determination of alder ecophysiological parameters within uplands of the Bonanza Creek Experimental Forest. Each replicate was visited once during the following dates.

	1997	**1998**
Sampling period 1	19 June – 3 July	11 June – 25 June
Sampling period 2	28 July – 9 Aug.	4 July – 21 July
Sampling period 3	3 Sept. – 30 Sept.	3 Aug. – 17 Aug.
Sampling period 4		3 Sept. – 24 Sept.

TABLE 2. Soil physical characteristics for upland forest stages within the Bonanza Creek Experimental Forest. Organic soils are combined Oi, Oe, and Oa horizons. Mineral soils are combined A and C mineral horizons. BD = bulk density. Values are means ± 1 SE (N = 34).

Parameter	**Post-fire**	**Mid-succession**	**White spruce**
Organic BD (g cm^{-3})	0.16 ± 0.03	0.12 ± 0.02	0.15 ± 0.02
Mineral BD (g cm^{-3})	0.89 ± 0.06	0.79 ± 0.02	0.84 ± 0.04
Organic (kg m^{-2})	9.59 ± 1.49	7.97 ± 0.31	10.81 ± 1.42
Mineral (kg m^{-2})	122.2 ± 13.7	101.3 ± 6.10	105.7 ± 3.3

TABLE 3. Soil chemical characteristics for upland forest stages within the Bonanza Creek Experimental Forest. Total = combined soil horizons to 20 cm, O = organic horizon, A = A mineral horizon, C = C mineral horizon, C:N = soil carbon to nitrogen ratio. Numbers within rows followed by different letters are significantly different at $P < 0.05$. Significant ANOVAs are in bold font. Values are means ± 1 SE (N = 34).

Parameter	Post-fire	Mid-succession	White spruce	ANOVA
Organic soil				
Mass (g m^{-2})	**9965 ± 988^{ab}**	**7937 ± 656^{b}**	**11029 ± 657^{a}**	**$F_{2,94} = 3.45$, $P < 0.05$**
Thickness (cm)	6.29 ± 0.36^{a}	7.00 ± 0.42^{a}	7.26 ± 0.36^{a}	$F_{2,96} = 2.21$, $P = 0.12$
Carbon				
Total (g m^{-2})	**3674 ± 246^{b}**	**3901 ± 217^{b}**	**4820 ± 203^{a}**	**$F_{2,90} = 7.88$, $P < 0.005$**
O (g m^{-2})	**1842 ± 189^{b}**	**1938 ± 156^{b}**	**2563 ± 154^{a}**	**$F_{2,90} = 5.92$, $P < 0.005$**
A (g m^{-2})	1114 ± 90^{a}	911 ± 94^{a}	1153 ± 119^{a}	$F_{2,90} = 1.61$, $P = 0.21$
C (g m^{-2})	974 ± 82^{a}	1052 ± 82^{a}	1185 ± 120^{a}	$F_{2,79} = 2.07$, $P = 0.13$
O (%)	**19.56 ± 1.49^{b}**	**24.69 ± 0.97^{a}**	**25.17 ± 1.33^{a}**	**$F_{2,90} = 7.21$ $P < 0.005$**
A (%)	**2.55 ± 0.32^{b}**	**3.81 ± 0.37^{ab}**	**3.90 ± 0.37^{a}**	**$F_{2,90} = 5.38$, $P < 0.05$**
C (%)	**1.25 ± 0.09^{a}**	**1.42 ± 0.10^{a}**	**1.57 ± 0.18^{a}**	**$F_{2,79} = 3.40$, $P < 0.05$**
Nitrogen				
Total (g m^{-2})	**242 ± 13^{ab}**	**209 ± 12^{b}**	**274 ± 14^{a}**	**$F_{2,90} = 4.54$, $P < 0.05$**
O (g m^{-2})	94.0 ± 10.0^{a}	90 ± 7^{a}	117 ± 7^{a}	$F_{2,90} = 2.90$, $P < 0.10$
A (g m^{-2})	**89 ± 10^{a}**	**51 ± 4^{b}**	**83 ± 13^{ab}**	**$F_{2,90} = 3.76$, $P < 0.05$**
C (g m^{-2})	79 ± 8^{a}	68 ± 5^{a}	79 ± 7^{a}	$F_{2,79} = 1.10$, $P = 0.34$
O (%)	1.00 ± 0.07^{a}	1.14 ± 0.05^{a}	1.14 ± 0.06^{a}	$F_{2,90} = 2.18$, $P = 0.12$
A (%)	**0.17 ± 0.01^{b}**	**0.22 ± 0.02^{ab}**	**0.27 ± 0.03^{a}**	**$F_{2,90} = 5.08$, $P < 0.05$**
C (%)	0.10 ± 0.01^{a}	0.09 ± 0.01^{a}	0.11 ± 0.01^{a}	$F_{2,79} = 0.96$, $P = 0.40$
Phosphorus				
Total (g m^{-2})	**79 ± 2^{a}**	**54 ± 3^{b}**	**44 ± 3^{c}**	**$F_{2,90} = 46.54$, $P < 0.0001$**
O (g m^{-2})	9 ± 0^{a}	7 ± 0^{a}	8 ± 0^{a}	$F_{2,90} = 1.58$, $P = 0.21$
A (g m^{-2})	**34 ± 3^{a}**	**14 ± 1^{b}**	**14 ± 2^{b}**	**$F_{2,90} = 23.38$, $P < 0.0001$**
C (g m^{-2})	**47 ± 3^{a}**	**32 ± 2^{b}**	**23 ± 2^{c}**	**$F_{2,79} = 27.28$, $P < 0.0001$**
O (%)	**0.10 ± 0.00^{a}**	**0.09 ± 0.00^{ab}**	**0.08 ± 0.01^{b}**	**$F_{2,90} = 5.78$, $P < 0.005$**
A (%)	**0.06 ± 0.00^{a}**	**0.06 ± 0.00^{a}**	**0.04 ± 0.00^{b}**	**$F_{2,90} = 10.63$, $P < 0.0001$**
C (%)	**0.06 ± 0.00^{a}**	**0.04 ± 0.00^{b}**	**0.03 ± 0.00^{c}**	**$F_{2,79} = 30.17$, $P < 0.0001$**
Soil CN				
Total	**15.23 ± 0.55^{b}**	**19.06 ± 0.79^{a}**	**18.29 ± 0.73^{a}**	**$F_{2,9} = 11.23$, $P < 0.0001$**
O	**19.63 ± 0.68^{b}**	**22.10 ± 0.83^{a}**	**22.22 ± 0.64^{a}**	**$F_{2,90} = 5.65$, $P < 0.005$**
A	**14.10 ± 0.83^{b}**	**18.56 ± 1.50^{a}**	**16.28 ± 1.01^{ab}**	**$F_{2,90} = 3.92$, $P < 0.05$**
C	**12.77 ± 0.59^{b}**	**16.84 ± 1.32^{a}**	**15.35 ± 1.02^{ab}**	**$F_{2,90} = 3.38$, $P < 0.05$**
pH				
O	5.75 ± 0.09^{a}	5.68 ± 0.05^{a}	5.59 ± 0.10^{a}	$F_{2,90} = 1.70$, $P = 0.19$
A	5.12 ± 0.08^{a}	4.98 ± 0.07^{a}	5.12 ± 0.09^{a}	$F_{2,90} = 1.10$, $P = 0.34$
C	**5.08 ± 0.05^{b}**	**5.33 ± 0.08^{a}**	**5.15 ± 0.06^{b}**	**$F_{2,90} = 4.34$, $P < 0.05$**

TABLE 4. Selected vegetation parameters of *A. viridis* in upland forest stages within the Bonanza Creek Experimental Forest. Statistical notations follow Table 3. Values for alder density measures are means ± 1 SE (N = 9). Values for alder canopy area are means ± 1 SE (N = 3).

Parameter	**Post-fire**	**Mid-succession**	**White spruce**	**ANOVA**
Stems shrub^{-1}	**21.06 ± 2.21^{a}**	**5.13 ± 0.35^{c}**	**13.13 ± 1.27^{b}**	**$F_{2,26} = 29.29$, $P < 0.0001$**
Shrubs ha^{-1}	**90.00 ± 9.86^{c}**	**178.89 ± 30.07^{b}**	**290.00 ± 62.32^{a}**	**$F_{2,26} = 20.08$, $P < 0.0001$**
Stems ha^{-1}	**1805.56 ± 175.46^{b}**	**897.78 ± 162.5^{c}**	**3630.00 ± 720.42^{a}**	**$F_{2,26} = 31.34$, $P < 0.0001$**
Alder canopy cover (m^2 ha^{-1})	1724.83 ± 321.54^{a}	3000.61 ± 722.06^{a}	5057.89 ± 1981.20^{a}	$F_{2,8} = 1.86$, $P = 0.23$

TABLE 5. Soil chemical characteristics under *A. viridis* canopies compared to interspace across upland forest stages within the Bonanza Creek Experimental Forest. Total = combined soil horizons to 20 cm, O = organic horizon, A = A mineral horizon, C = C mineral horizon, C:N = total soil carbon to nitrogen ratio. Statistical notations follow Table 3. Values are means ± 1 SE (N = 50).

Parameter	Sub-canopy	Interspace	ANOVA
Organic soil			
Mass (g m^{-2})	9250 ± 639[a]	10014 ± 698[a]	$F_{1,96} = 1.51$, $P = 0.22$
Thickness (cm)	7.09 ± 0.34[a]	6.58 ± 0.30[a]	$F_{1,94} = 0.74$, $P = 0.39$
Carbon			
Total (g m^{-2})	4220 ± 195[a]	3992 ± 198[a]	$F_{1,90} = 1.07$, $P = 0.30$
O (g m^{-2})	2191 ± 155[a]	2007 ± 135[a]	$F_{1,90} = 1.04$, $P = 0.31$
A (g m^{-2})	1117 ± 91[a]	1005 ± 74[a]	$F_{1,90} = 0.66$, $P = 0.42$
C (g m^{-2})	1022 ± 66[a]	1122 ± 89[a]	$F_{1,79} = 0.36$, $P = 0.55$
O (%)	**24.40 ± 1.03[a]**	**21.56 ± 1.18[b]**	**$F_{1,90} = 5.04$, $P < 0.05$**
A (%)	3.40 ± 0.28[a]	3.35 ± 0.32[a]	$F_{1,90} = 0.11$, $P = 0.74$
C (%)	1.41 ± 0.08[a]	1.42 ± 0.13[a]	$F_{1,73} = 0.04$, $P = 0.85$
Nitrogen			
Total (g m^{-2})	246 ± 11[a]	237 ± 11[a]	$F_{1,90} = 0.24$, $P = 0.62$
O (g m^{-2})	105 ± 8[a]	95 ± 6[a]	$F_{1,90} = 1.15$, $P = 0.29$
A (g m^{-2})	75 ± 7[a]	74 ± 9[a]	$F_{1,90} = 0.01$, $P = 0.92$
C (g m^{-2})	73 ± 4[a]	77 ± 6[a]	$F_{1,79} = 0.31$, $P = 0.58$
O (%)	**1.16 ± 0.05[a]**	**1.02 ± 0.05[b]**	**$F_{1,90} = 6.56$, $P < 0.05$**
A (%)	0.22 ± 0.02[a]	0.21 ± 0.02[a]	$F_{1,90} = 0.15$, $P = 0.70$
C (%)	0.10 ± 0.01[a]	0.10 ± 0.01[a]	$F_{1,79} = 0.24$, $P = 0.62$
Phosphorus			
Total (g m^{-2})	**57 ± 3[a]**	**63 ± 3[b]**	**$F_{1,90} = 4.96$, $P < 0.05$**
O (g m^{-2})	7 ± 0[a]	8 ± 0[a]	$F_{1,90} = 1.70$, $P = 0.20$
A (g m^{-2})	22 ± 2[a]	21 ± 2[a]	$F_{1,90} = 0.00$, $P = 0.95$
C (g m^{-2})	**30 ± 2[a]**	**37 ± 2[b]**	**$F_{1,79} = 5.79$, $P < 0.05$**
O (%)	0.09 ± 0.00[a]	0.09 ± 0.00[a]	$F_{1,90} = 0.95$, $P = 0.33$
A (%)	0.05 ± 0.00[a]	0.06 ± 0.00[a]	$F_{1,90} = 0.36$, $P = 0.55$
C (%)	0.04 ± 0.00[a]	0.05 ± 0.00[a]	$F_{1,79} = 1.38$, $P = 0.24$
Soil C:N			
Total (g m^{-2})	17.60 ± 0.66[a]	17.24 ± 0.56[a]	$F_{1,90} = 0.54$, $P = 0.47$
O	21.26 ± 0.57[a]	21.19 ± 0.65[a]	$F_{1,90} = 0.05$, $P = 0.83$
A	16.75 ± 1.16[a]	15.70 ± 0.71[a]	$F_{1,90} = 0.81$, $P = 0.37$
C	14.84 ± 0.97[a]	15.38 ± 0.83[a]	$F_{1,79} = 0.00$, $P = 0.95$
pH			
O	5.60 ± 0.06[a]	5.75 ± 0.08[a]	$F_{1,90} = 2.45$, $P = 0.12$
A	4.99 ± 0.06[a]	5.16 ± 0.07[a]	$F_{1,90} = 3.38$, $P < 0.10$
C	**5.11 ± 0.06[a]**	**5.28 ± 0.06[b]**	**$F_{1,79} = 6.72$, $P < 0.05$**

TABLE 6. Soil chemical characteristics under *A. viridis* canopies compared to interspace for (A) post-fire, (B) mid-succession and (C) white spruce upland forest stages within Bonanza Creek Experimental Forest. Total = combined soil horizons to 20 cm, O = organic horizon, A = A mineral horizon, C = C mineral horizon, C:N = total soil carbon to nitrogen ratio. Statistical notations follow Table 3. Values are means ± 1 SE (N = 17).

TABLE 6A.

Parameter	Subcanopy	Interspace	ANOVA
Organic soil			
Mass (g m^{-2})	10143 ± 1487[a]	9787 ± 1348[a]	$F_{1,33} = 0.38$, $P = 0.54$
Thickness (cm)	6.50 ± 0.59[a]	6.09 ± 0.44[a]	$F_{1,33} = 0.03$, $P = 0.85$
Carbon			
Total (g m^{-2})	4000 ± 401[a]	3347 ± 275[a]	$F_{1,33} = 1.90$, $P = 0.18$
O (g m^{-2})	2126 ± 303[a]	1558 ± 215[a]	$F_{1,33} = 2.39$, $P = 0.13$
A (g m^{-2})	1233 ± 134[a]	996 ± 119[a]	$F_{1,33} = 1.75$, $P = 0.20$
C (g m^{-2})	907 ± 121[a]	1036 ± 114[a]	$F_{1,24} = 0.40$, $P = 0.53$
O (%)	21.85 ± 2.00[a]	17.27 ± 2.14[a]	$F_{1,33} = 3.31$, $P < 0.10$
A (%)	2.59 ± 0.47[a]	2.52 ± 0.47[a]	$F_{1,33} = 0.90$, $P = 0.90$
C (%)	1.26 ± 0.15[a]	1.24 ± 0.11[a]	$F_{1,24} = 0.82$, $P = 0.45$
Nitrogen			
Total (g m^{-2})	258 ± 21[a]	225 ± 16[a]	$F_{1,33} = 1.40$, $P = 0.25$
O (g m^{-2})	106 ± 17[a]	82 ± 10[a]	$F_{1,33} = 1.52$, $P = 0.23$
A (g m^{-2})	102 ± 15[a]	76 ± 12[a]	$F_{1,33} = 1.65$, $P = 0.21$
C (g m^{-2})	71 ± 9[a]	86 ± 13[a]	$F_{1,24} = 0.62$, $P = 0.44$
O (%)	1.08 ± 0.10[a]	0.93 ± 0.10[a]	$F_{1,33} = 1.79$, $P = 0.19$
A (%)	0.18 ± 0.02[a]	0.16 ± 0.02[a]	$F_{1,33} = 0.48$, $P = 0.49$
C (%)	0.10 ± 0.01[a]	0.10 ± 0.01[a]	$F_{1,24} = 0.03$, $P = 0.87$
Phosphorus			
Total (g m^{-2})	76.0 ± 3.0[a]	81.0 ± 4.0[a]	$F_{1,33} = 0.88$, $P = 0.35$
O (g m^{-2})	8.00 ± 0.0[a]	9.00 ± 1.0[a]	$F_{1,33} = 0.32$, $P = 0.58$
A (g m^{-2})	36.0 ± 5.0[a]	32.0 ± 5.0[a]	$F_{1,33} = 0.27$, $P = 0.61$
C (g m^{-2})	44.0 ± 4.0[a]	51.0 ± 5.0[a]	$F_{1,24} = 1.06$, $P = 0.45$
O (%)	0.09 ± 0.00[a]	0.10 ± 0.00[a]	$F_{1,33} = 2.10$, $P = 0.16$
A (%)	0.06 ± 0.00[a]	0.07 ± 0.00[a]	$F_{1,33} = 0.69$, $P = 0.41$
C (%)	0.06 ± 0.00[a]	0.06 ± 0.01[a]	$F_{1,24} = 0.01$, $P = 0.91$

TABLE 6A CONTINUED.

Parameter	Subcanopy	Interspace	ANOVA
C:N			
Total	15.51 ± 0.85[a]	14.96 ± 0.73[a]	$F_{1,33} = 0.24$, $P = 0.63$
O	20.70 ± 0.97[a]	18.55 ± 0.90[a]	$F_{1,33} = 2.63$, $P = 0.12$
A	13.56 ± 1.13[a]	14.64 ± 1.24[a]	$F_{1,33} = 0.80$, $P = 0.38$
C	12.73 ± 0.86[a]	12.81 ± 0.84[a]	$F_{1,24} = 0.00$, $P = 0.98$
pH			
O	**5.58 ± 0.10[b]**	**5.92 ± 0.15[a]**	**$F_{1,33} = 5.09$, $P < 0.05$**
A	**4.95 ± 0.05[b]**	**5.30 ± 0.14[a]**	**$F_{1,33} = 6.98$, $P < 0.05$**
C	**5.00 ± 0.05[b]**	**5.18 ± 0.09[a]**	**$F_{1,24} = 4.82$, $P < 0.05$**

TABLE 6 CONTINUED. Soil chemical characteristics under *A. viridis* canopies compared to interspace for (A) post-fire, (B) mid-succession and (C) white spruce upland forest stages within Bonanza Creek Experimental Forest. Total = combined soil horizons to 20 cm, O = organic horizon, A = A mineral horizon, C = C mineral horizon, C:N = total soil carbon to nitrogen ratio. Statistical notations follow Table 3. Values are means ± 1 SE (N = 17).

TABLE 6B.

Parameter	Subcanopy	Interspace	ANOVA
Organic soil			
Mass (g m^{-2})	7692 ± 797[a]	8183 ± 1065[a]	$F_{1,33} = 0.26$, $P = 0.61$
Thickness (cm)	7.21 ± 0.67[a]	6.76 ± 0.53[a]	$F_{1,33} = 0.13$, $P = 0.72$
Carbon			
Total (g m^{-2})	3890 ± 293[a]	3912 ± 330[a]	$F_{1,29} = 0.00$, $P = 0.96$
O (g m^{-2})	1928 ± 249[a]	1947 ± 199[a]	$F_{1,29} = 0.00$, $P = 0.95$
A (g m^{-2})	848 ± 116[a]	973 ± 152[a]	$F_{1,29} = 0.42$, $P = 0.52$
C (g m^{-2})	1113 ± 115[a]	991 ± 119[a]	$F_{1,29} = 0.65$, $P = 0.43$
O (%)	25.06 ± 1.26[a]	24.33 ± 1.50[a]	$F_{1,29} = 0.15$, $P = 0.70$
A (%)	3.86 ± 0.45[a]	3.76 ± 0.60[a]	$F_{1,29} = 0.02$, $P = 0.88$
C (%)	1.54 ± 0.14[a]	1.29 ± 0.15[a]	$F_{1,29} = 2.00$, $P = 0.17$
Nitrogen			
Total (g m^{-2})	203 ± 16[a]	215 ± 18[a]	$F_{1,29} = 0.32$, $P = 0.58$
O (g m^{-2})	88 ± 12[a]	91 ± 10[a]	$F_{1,29} = 0.06$, $P = 0.80$
A (g m^{-2})	43 ± 4[a]	59 ± 8[a]	$F_{1,29} = 3.09$, $P < 0.10$
C (g m^{-2})	72 ± 8[a]	64 ± 8[a]	$F_{1,29} = 0.57$, $P = 0.46$
O (%)	1.15 ± 0.06[a]	1.14 ± 0.08[a]	$F_{1,29} = 0.01$, $P = 0.92$
A (%)	0.22 ± 0.04[a]	0.22 ± 0.03[a]	$F_{1,29} = 0.02$, $P = 0.90$
C (%)	0.10 ± 0.01[a]	0.08 ± 0.01[a]	$F_{1,29} = 1.37$, $P = 0.25$
Phosphorus			
Total (g m^{-2})	**47 ± 3[b]**	**61 ± 4[a]**	**$F_{1,29} = 5.82$, $P < 0.05$**
O (g m^{-2})	6 ± 0[a]	8 ± 1[a]	$F_{1,29} = 1.55$, $P = 0.22$
A (g m^{-2})	12 ± 2[a]	16 ± 1[a]	$F_{1,29} = 1.54$, $P = 0.23$
C (g m^{-2})	**28 ± 2[b]**	**37 ± 3[a]**	**$F_{1,29} = 4.93$, $P < 0.05$**
O (%)	0.09 ± 0.00[a]	0.10 ± 0.00[a]	$F_{1,29} = 2.48$, $P = 0.13$
A (%)	0.05 ± 0.01[a]	0.06 ± 0.01[a]	$F_{1,29} = 0.63$, $P = 0.44$
C (%)	0.04 ± 0.00[a]	0.05 ± 0.00[a]	$F_{1,29} = 0.18$, $P = 1.93$

TABLE 6B CONTINUED.

Parameter	Subcanopy	Interspace	ANOVA
C:N			
Total	19.8 ± 1.45[a]	18.31 ± 0.63[a]	$F_{1,29} = 1.04$, $P = 0.32$
O	22.28 ± 1.26[a]	21.89 ± 1.14[a]	$F_{1,29} = 0.08$, $P = 0.78$
A	20.76 ± 2.74[a]	16.35 ± 1.10[a]	$F_{1,29} = 2.23$, $P = 0.15$
C	17.18 ± 2.2[a]	16.51 ± 1.54[a]	$F_{1,29} = 0.06$, $P = 0.80$
pH			
O	5.67 ± 0.06[a]	5.68 ± 0.09[a]	$F_{1,29} = 0.01$, $P = 0.90$
A	4.92 ± 0.09[a]	5.04 ± 0.11[a]	$F_{1,29} = 0.72$, $P = 0.40$
C	5.23 ± 0.12[a]	5.44 ± 0.11[a]	$F_{1,29} = 2.12$, $P = 0.16$

TABLE 6 CONTINUED. Soil chemical characteristics under *A. viridis* canopies compared to interspace for (A) post-fire, (B) mid-succession and (C) white spruce upland forest stages within Bonanza Creek Experimental Forest. Total = combined soil horizons to 20 cm, O = organic horizon, A = A mineral horizon, C = C mineral horizon, C:N = total soil carbon to nitrogen ratio. Statistical notations follow Table 3. Values are means ± 1 SE (N = 17).

TABLE 6C.

Parameter	Subcanopy	Interspace	ANOVA
Organic soil			
Mass (g m^{-2})	**9899 ± 718^{b}**	**12087 ± 1034^{a}**	**$F_{1,28} = 4.75$, $P < 0.05$**
Thickness (cm)	7.63 ± 0.43^{a}	6.91 ± 0.57^{a}	$F_{1,28} = 1.24$, $P = 0.28$
Carbon			
Total (g m^{-2})	4842 ± 223^{a}	4801 ± 340^{a}	$F_{1,26} = 0.06$, $P = 0.81$
O (g m^{-2})	2550 ± 222^{a}	2575 ± 222^{a}	$F_{1,26} = 0.00$, $P = 0.98$
A (g m^{-2})	1266 ± 209^{a}	1048 ± 126^{a}	$F_{1,26} = 0.50$, $P = 0.49$
C (g m^{-2})	1024 ± 111^{a}	1358 ± 213^{a}	$F_{1,24} = 1.42$, $P = 0.25$
O (%)	26.79 ± 1.77^{a}	23.67 ± 1.95^{a}	$F_{1,26} = 2.14$, $P = 0.16$
A (%)	3.92 ± 0.49^{a}	3.89 ± 0.57^{a}	$F_{1,26} = 0.08$, $P = 0.77$
C (%)	1.41 ± 0.11^{a}	1.75 ± 0.35^{a}	$F_{1,24} = 0.42$, $P = 0.52$
Nitrogen			
Total (g m^{-2})	277 ± 14^{a}	271 ± 24^{a}	$F_{1,26} = 0.00$, $P = 0.96$
O (g m^{-2})	122 ± 10^{a}	112 ± 10^{a}	$F_{1,26} = 0.44$, $P = 0.52$
A (g m^{-2})	78 ± 10^{a}	87 ± 23^{a}	$F_{1,26} = 0.39$, $P = 0.54$
C (g m^{-2})	76 ± 6^{a}	82 ± 12^{a}	$F_{1,24} = 0.73$, $P = 0.40$
O (%)	**1.28 ± 0.07^{a}**	**1.01 ± 0.07^{b}**	**$F_{1,26} = 9.80$, $P < 0.005$**
A (%)	0.27 ± 0.03^{a}	0.27 ± 0.04^{a}	$F_{1,26} = 0.00$, $P = 0.96$
C (%)	0.11 ± 0.01^{a}	0.10 ± 0.02^{a}	$F_{1,24} = 0.01$, $P = 0.92$
Phosphorus			
Total (g m^{-2})	43 ± 5^{a}	45 ± 3^{a}	$F_{1,26} = 0.12$, $P = 0.73$
O (g m^{-2})	7 ± 0^{a}	8 ± 0^{a}	$F_{1,26} = 0.24$, $P = 0.63$
A (g m^{-2})	14 ± 3^{a}	14 ± 2^{a}	$F_{1,26} = 0.18$, $P = 0.68$
C (g m^{-2})	20 ± 2^{a}	25 ± 3^{a}	$F_{1,24} = 3.21$, $P < 0.10$
O (%)	0.08 ± 0.01^{a}	0.08 ± 0.01^{a}	$F_{1,26} = 1.73$, $P = 0.20$
A (%)	0.04 ± 0.00^{a}	0.04 ± 0.00^{a}	$F_{1,26} = 0.78$, $P = 0.39$
C (%)	0.03 ± 0.00^{a}	0.03 ± 0.00^{a}	$F_{1,24} = 0.31$, $P = 0.59$

TABLE 6C CONTINUED.

Parameter	Subcanopy	Interspace	ANOVA
C:N			
Total	17.80 ± 0.76[a]	18.76 ± 1.24[a]	$F_{1,26} = 0.12$, $P = 0.73$
O	**20.86 ± 0.54[b]**	**23.49 ± 1.03[a]**	$\mathbf{F_{1,26} = 5.04}$, $\mathbf{P < 0.05}$
A	16.31 ± 1.54[a]	16.25 ± 1.38[a]	$F_{1,26} = 0.02$, $P = 0.90$
C	14.15 ± 1.23[a]	16.64 ± 1.59[a]	$F_{1,24} = 0.38$, $P = 0.54$
pH			
O	5.54 ± 0.13[a]	5.64 ± 0.15[a]	$F_{1,26} = 0.02$, $P = 0.89$
A	5.12 ± 0.15[a]	5.12 ± 0.10[a]	$F_{1,26} = 0.17$, $P = 0.69$
C	5.10 ± 0.08[a]	5.21 ± 0.08[a]	$F_{1,24} = 1.80$, $P = 0.19$

TABLE 7. *A. viridis* foliar parameters and nutrient resorption from senescent leaves for both study years combined in upland forest stages within the Bonanza Creek Experimental Forest. SLW = specific leaf weight. Statistical notations follow Table 3. Values for maximum and senescent foliar parameters are means ± 1 SE (N = 60). Values for resorption pools and resorption efficiency are means ± 1 SE (N = 6).

Parameter	**Post-fire**	**Mid-succession**	**White spruce**	**ANOVA**
Maximum SLW (g m^{-2})	67.35 ± 3.78^{a}	39.31 ± 4.40^{b}	37.08 ± 3.77^{b}	$F_{2,17} = 270.28$, $P < 0.001$
Nitrogen				
Maximum (%)	2.71 ± 0.09^{ab}	2.69 ± 0.05^{b}	2.86 ± 0.03^{a}	$F_{2,17} = 5.55$, $P < 0.05$
Maximum (g m^{-2})	1.82 ± 0.10^{a}	1.05 ± 0.11^{b}	1.03 ± 0.10^{b}	$F_{2,17} = 239.31$, $P < 0.0001$
Senescent (g m^{-2})	1.14 ± 0.11^{a}	0.82 ± 0.05^{b}	0.75 ± 0.08^{b}	$F_{2,17} = 8.10$, $P < 0.005$
Resorption pool (g m^{-2})	0.68 ± 0.11^{a}	0.23 ± 0.07^{b}	0.28 ± 0.10^{b}	$F_{2,17} = 9.80$, $P < 0.005$
Resorption efficiency (%)	36.92 ± 5.55^{a}	19.43 ± 4.45^{a}	25.99 ± 7.42^{a}	$F_{2,17} = 2.41$, $P = 0.13$
Phosphorus				
Maximum (%)	0.27 ± 0.04^{a}	0.21 ± 0.01^{b}	0.23 ± 0.01^{b}	$F_{2,17} = 13.76$, $P < 0.005$
Maximum (g m^{-2})	0.17 ± 0.02^{a}	0.08 ± 0.01^{b}	0.08 ± 0.01^{b}	$F_{2,17} = 148.07$, $P < 0.0001$
Senescent (g m^{-2})	0.16 ± 0.03^{a}	0.06 ± 0.01^{b}	0.05 ± 0.01^{b}	$F_{2,17} = 20.32$, $P < 0.005$
Resorption pool (g m^{-2})	0.02 ± 0.01^{a}	0.02 ± 0.01^{a}	0.03 ± 0.01^{a}	$F_{2,17} = 0.91$, $P = 0.10$
Resorption efficiency (%)	15.58 ± 8.8^{a}	25.53 ± 7.43^{a}	32.89 ± 8.01^{a}	$F_{2,17} = 1.18$, $P = 0.36$

TABLE 8. *A. viridis* foliar parameters and nutrient resorption from senescent leaves by study year in upland forest stages within the Bonanza Creek Experimental Forest. SLW = specific leaf weight. Statistical notations follow Table 3. Values for maximum and senescent foliar parameters are means ± 1 SE (N = 30). Values for resorption pools and resorption efficiency are means ± 1 SE (N = 3).

Parameter		**Post-fire**	**Mid-succession**	**White spruce**
Maximum SLW ($g\ m^{-2}$)	1997	**59.23 ± 1.52^{b}**	**29.63 ± 1.24^{b}**	**28.93 ± 0.55^{b}**
	1998	**75.48 ± 1.75^{a}**	**48.98 ± 1.34^{a}**	**45.23 ± 2.05^{a}**
	ANOVA	**$F_{1,5} = 49.36$, $P < 0.005$**	**$F_{1,5} = 112.68$, $P < 0.0005$**	**$F_{1,5} = 88.28$, $P < 0.05$**
Maximum leaf % N	1997	2.77 ± 0.12^{a}	$2.74 \pm 0.01a$	2.83 ± 0.06^{a}
	1998	2.64 ± 0.15^{a}	$2.64 \pm 0.09a$	2.90 ± 0.03^{a}
	ANOVA	$F_{1,5} = 6.32$, $P = 0.13$	$F_{1,5} = 1.20$, $P = 0.39$	$F_{1,5} = 1.07$, $P = 0.41$
Maximum leaf N ($g\ m^{-2}$)	1997	**1.63 ± 0.03^{b}**	**0.81 ± 0.04^{b}**	**0.82 ± 0.01^{b}**
	1998	**2.01 ± 0.10^{a}**	**1.29 ± 0.05^{a}**	**1.23 ± 0.06^{a}**
	ANOVA	**$F_{1,5} = 13.16$, $P < 0.05$**	**$F_{1,5} = 61.46$, $P < 0.005$**	**$F_{1,5} = 38.13$, $P < 0.005$**
Senescent leaf N ($g\ m^{-2}$)	1997	1.05 ± 0.16^{a}	**0.73 ± 0.02^{b}**	0.64 ± 0.10^{a}
	1998	1.23 ± 0.16^{a}	**0.92 ± 0.06^{a}**	0.85 ± 0.11^{a}
	ANOVA	$F_{1,5} = 0.31$, $P = 0.63$	**$F_{1,5} = 7.71$, $P = 0.05$**	$F_{1,5} = 1.17$, $P = 0.40$
N resorption ($g\ m^{-2}$)	1997	0.57 ± 0.19^{a}	**0.08 ± 0.02^{b}**	0.18 ± 0.09^{a}
	1998	0.78 ± 0.11^{a}	**0.37 ± 0.02^{a}**	0.38 ± 0.17^{a}
	ANOVA	$F_{1,5} = 0.90$, $P = 0.40$	**$F_{1,5} = 140.25$, $P < 0.005$**	$F_{1,5} = 1.00$, $P = 0.37$
N efficiency (%)	1997	34.85 ± 10.84^{a}	**9.94 ± 1.81^{b}**	22.49 ± 11.22^{a}
	1998	39.00 ± 5.70^{a}	**28.92 ± 2.43^{a}**	29.49 ± 11.72^{a}
	ANOVA	$F_{1,5} = 0.06$, $P = 0.91$	**$F_{1,5} = 39.15$, $P < 0.005$**	$F_{1,5} = 0.10$, $P = 0.78$

TABLE 8 (CONTINUED). *A. viridis* foliar parameters and nutrient resorption from senescent leaves by study year in upland forest stages within Bonanza Creek Experimental Forest. SLW = specific leaf weight. Statistical notations follow Table 3. Values for maximum and senescent foliar parameters are means ± 1 SE (N = 30). Values for resorption pools and resorption efficiency are means ± 1 SE (N = 3).

Parameter		**Post-fire**	**Mid-succession**	**White spruce**
Maximum leaf % P	1997	0.24 ± 0.04^{a}	0.19 ± 0.01^{a}	$\mathbf{0.21 \pm 0.01^{b}}$
	1998	0.30 ± 0.07^{a}	0.22 ± 0.01^{a}	$\mathbf{0.25 \pm 0.02^{a}}$
	ANOVA	$F_{1,5} = 3.95$, $P = 0.19$	$F_{1,5} = 6.06$, $P = 0.10$	$\mathbf{F_{1,5} = 103.29, P < 0.05}$
Maximum leaf P (g m^{-2})	1997	$\mathbf{0.14 \pm 0.02^{a}}$	$\mathbf{0.05 \pm 0.01^{b}}$	$\mathbf{0.06 \pm 0.00^{a}}$
	1998	$\mathbf{0.20 \pm 0.03^{b}}$	$\mathbf{0.10 \pm 0.01^{a}}$	$\mathbf{0.10 \pm 0.00^{b}}$
	ANOVA	$\mathbf{F_{1,5} = 26.38, P < 0.05}$	$\mathbf{F_{1,5} = 27.84, P < 0.005}$	$\mathbf{F_{1,5} = 38.08, P < 0.005}$
Senescent leaf P (g m^{-2})	1997	0.12 ± 0.04^{a}	0.05 ± 0.00^{a}	$\mathbf{0.04 \pm 0.01^{b}}$
	1998	0.19 ± 0.05^{a}	0.07 ± 0.01^{a}	$\mathbf{0.07 \pm 0.00^{a}}$
	ANOVA	$F_{1,5} = 2.44$, $P = 0.26$	$F_{1,5} = 2.61$, $P = 0.25$	$\mathbf{F_{1,5} = 13.01, P < 0.05}$
P resorption (g m^{-2})	1997	0.02 ± 0.02^{a}	0.01 ± 0.01^{b}	0.02 ± 0.01^{a}
	1998	0.02 ± 0.02^{a}	0.03 ± 0.01^{a}	0.03 ± 0.00^{b}
	ANOVA	$F_{1,5} = 0.00$, $P = 0.96$	$F_{1,5} = 6.67$, $P < 0.10$	$F_{1,5} = 1.32$, $P = 0.37$
P efficiency (%)	1997	17.06 ± 13.66^{a}	15.47 ± 8.20^{a}	34.48 ± 17.65^{a}
	1998	14.09 ± 14.09^{a}	35.60 ± 10.37^{a}	31.31 ± 2.69^{a}
	ANOVA	$F_{1,5} = 0.02$, $P = 0.91$	$F_{1,5} = 4.24$, $P = 0.20$	$F_{1,5} = 0.04$, $P = 0.85$

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